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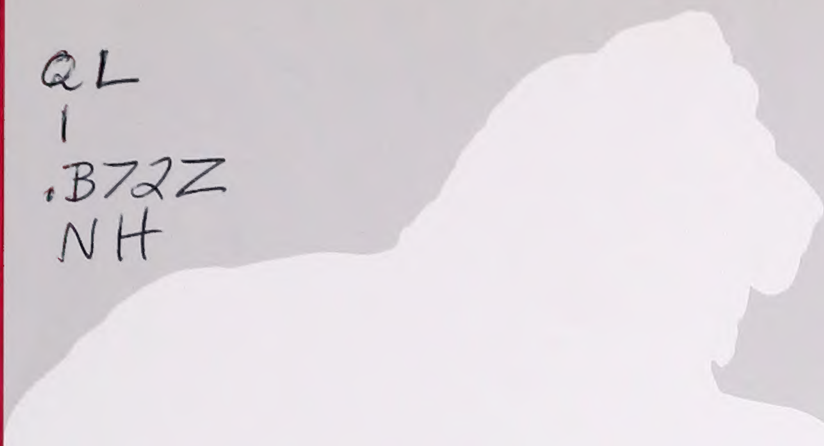

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Editorial

On occasion of his 66th birthday and his retirement from his position as curator of herpetology after nearly 40 years at the Museum Alexander Koenig, I had the great pleasure to be the editor of a Festschrift, and the co-ordinator of a colloquium honouring the work of Wolfgang Böhme.

The title of this special issue of the Bonn zoological Bulletin and the colloquium is a combination of *Herpetologia*, referring to several symposia (e.g. the two SEH meetings) he organized during his time at this institute, and *Koenigiana*, referring to 'his' museum.

During his time at curator from 1971 onwards, he increased the at this time 'sleeping' herpetological collection with less than 9500 specimens to one of the leading collections in Germany and Europe with about 100.000 vouchers. His scientific work is documented in more than 530 publications and with his enthusiasm he influenced and stimulated 32 PhD (ten more candidates are still working on their theses), 145 diploma and 35 state-examen students, some of them working today as scientists in renowned German and European institutions.

As his student, I was influenced since my first time at the University of Bonn and the Museum Koenig by his courses and lectures and he positively forced my decision to work with herpetological systematics and the Afrotropical region.

These influences Wolfgang Böhme had on many upcoming scientists and his numerous cooperations are in part reflected by the impressive set of articles about various topics published in the present issue of Bonn zoological Bulletin, written by friends, colleagues and former students. These articles are partly dealing with his main scientific fields of interests: Africa, chameleons, or monitor lizards, but also with 'side'-fields like lacertids, nomenclature or the history of herpetology. Many articles are first descriptions of new amphibian and reptile species named after Wolfgang Böhme, which are the 'living manifestations' of his impressive work. Moreover, the two non-herpetological articles show that he has also some impact in other zoological disciplines.

As guest editor, I would like to thank all the reviewers for their helpful comments. Without their fast work it would not have been possible to have this issue ready right in time. Especially, I would like to thank Brian Sinclair who did the English in review in some of the articles.

Ph. Wagner

Philipp Wagner (Guest Editor)

Bonn, November 2010

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Preface

This volume is dedicated to a scientist, who during the past four decades transformed the herpetology collection of Museum Koenig into one of the most prominent European research facilities for reptile systematics and biology. Under his management, the comparatively young collection of reptiles and amphibians in Bonn has grown tenfold and became one of the most important ones in Germany. Moreover, he dedicated his time and energy not only to science, but also to the development of the institute, which has been his second home. Thanks to his commitment and personality, he became the undisputed head of the vertebrate department, which he still leads today. He also was, and still is, the link between the museum and the many experts among laypersons, who contribute substantially to the growth of scientific knowledge and otherwise shy from direct contact with professionals. With the same spirit he cooperated with the Alexander Koenig Gesellschaft, the friends of the museum society.

Wolfgang Böhme is a passionate zoologist whose enthusiasm infected several generations of students, many of which later became successful scientists themselves. He regularly takes students on field courses, where he teaches them how to discover, observe and capture snakes, lizards and frogs, as well as identify other animals such as grasshoppers and bees. His favourite destination for this purpose has always been Lake Neusiedl that became a popular destination among biology students in Bonn.

Wolfgang Böhme frequently invited like-minded zoologists from other countries to work with him in Bonn or to attend German conferences, and it was obvious that he was thrilled for the opportunity to learn of other people's discoveries out of pure fascination by animals and without any jealousy.

During the past 40 years, the Museum's directors were grateful for his public-relations work. He frequently offered evening lectures for the general public with an enjoyable combination of adventure, discovery, and Böhme's characteristic humour. He authored popular articles for the media and for the institute's series "Tier und Museum" (later "Koenigiana"), a publication for which he acted as an editor. Similarly, he was always ready to take part in non-scientific events, where he participated in activities such as reading poems by his ancestor Wilhelm Busch, whose funny bone he obviously inherited.

With this volume on the occasion of his retirement from official duties, we want to thank him for his outstanding contribution to herpetology and to the development of Museum Koenig. I hope this is just the beginning of a new period of active research, for which we will always have a space available for him in our institute.

J. Wolfgang Wägele (Director)

Bonn, November 2010

Greetings from the SEH

I met Wolfgang Böhme for the first time at the very beginning of my carrier, just after my graduation. I remember that he was extremely friendly when talking about lizards, the Mediterranean basin and his deep love for Africa and the tropics, making my first impact with the international professional herpetological world easy and smooth. Throughout our long professional relationship, Wolfgang has always been extraordinarily open to new ideas, sharing research projects with a number of scientists worldwide and prompting the creation of a network of enthusiastic believers, such as for the circum-Mediterranean *Podarcis* fans. I remember very well the beginning of the "saga" of the Symposia on the Lacertids of the Mediterranean, together with Nicholas E. Arnold, Massimo Capula, Valentin Pérez-Mellado, Efstratios Valakos and, which is still successfully ongoing. In the nineties, as President of the *Societas Europaea Herpetologica*, Wolfgang Böhme put a tremendous effort into establishing collaborations between the national European herpetological societies. He also opened the doors of the herpetological collection of the Alexander Koenig Museum to a multitude of island zoologists, inducing the full scientific exploitation of such an extraordinary biological treasure. His outstanding scientific activity, together with his humanity and intellectual generosity make Wolfgang Böhme one of the reference point in and out my professional life and I'll always be grateful to him and his lovely family for such a warm and positive friendship.

Claudia Corti

(President *Societas Europaea Herpetologica*)

Bonn, November 2010

Greetings from the DGHT

On the occasion of the retirement of Prof. Dr. Wolfgang Böhme, curator of herpetology, head of the vertebrate department, and deputy director of the Zoologisches Forschungsmuseum Alexander Koenig, we were honoured with an invitation to direct a few words to the readers of this special issue of the Bonn Zoological Bulletin.

We sincerely appreciate this opportunity, as the name Wolfgang Böhme is not only connected to a distinguished career in herpetology, but also to a person who always made an effort to keep a close connection between professional scientific research and amphibian and reptile amateurs all over the world. Wolfgang Böhme's achievements in this particular field of interaction are not less than outstanding. There is probably no other herpetologist whose research benefited as much from data supplied by amateurs, and there are countless thankful amateurs whose pastime has been deeply enriched by the scientific advice and the stimulating attitude of Wolfgang Böhme. Sharing data, knowledge and specimens with people operating outside the scientific community was paramount for many spectacular discoveries and the furtherance of knowledge about the biology and ecology of amphibian and reptile species, many of which are considered to be well-known today. Decades ago, it was mainly these amateur enthusiasts who travelled to remote and previously unexplored exotic areas in search of their "pets" and returned with treasures of data and photographs that gave rise to subsequent research projects. It is Wolfgang Böhme's merit and strength to have fostered and encouraged this tradition of interaction for several decades.

Bringing professionals and amateurs together and promoting their dialog is also one main characteristic of the Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT), as is apparent by the society's name. As a consequence, there was, and is, some kind of "natural relationship" between Wolfgang Böhme and the DGHT, and this relationship has been a sustained and fruitful one. Shortly after he took his position at the Museum Koenig, he founded the "DGHT Stadtgruppe Bonn" in 1973. Later, Wolfgang Böhme became president of the society and held this position from 1983 to 1991. He was furthermore a founding member of the DGHT Work Group Literature and History, and a regular member of the Work Groups Chameleons and Lacertids. In 1994, Böhme was made an honorary member of the DGHT, and very recently, the current executive board asked him to join its advisory council. And so it is for many reasons that Böhme's name and personality are closely interlinked with the DGHT.

The DGHT as a society, DGHT members and associates, as well as many students and colleagues owe a lot to Wolfgang Böhme. Despite facing his 'official' retirement as a herpetologist now, we are convinced that few things will change and that his fruitful relationships with the DGHT will continue for many years to come. Dear Wolfgang Böhme, thank you for everything.

The DGHT executive board

(Peter Buchert, Jörn Köhler, Axel Kwet, Stefan Lötters, Wolfgang Schmidt, Holger Vetter)

Bonn, November 2010

Curriculum Vitae of Wolfgang Böhme

Born November 21, 1944 at Schönberg near Kiel (Schleswig-Holstein, Germany) as the 3rd child of the musician Ferdinand Böhme (1906–1971) and his wife Hedwig, born Stange (1913–1992). Ferdinand Böhme was violinist of the first desk at the municipal orchestra in the opera house of Kiel and subject teacher for violine, both privately and at the Pedagogic College of Kiel.

From a first marriage (1970–1974) father of one daughter (Judith). Since 1974 married with Roswitha Böhme. From this marriage two sons (Moritz and Peter).

Wolfgang Böhme finished highschool ("Kieler Gelehrtenschule") in Kiel, April 1965, and subsequently studied zoology, botany and paleontology at the "Christian-Albrechts-Universität" of Kiel. Doctoral degree with a thesis on hemipenis morphology in lacertid lizards in June 1971 under supervision of Prof. Dr. Wolf Herre.

From August 1971 until December 2010 head of the Herpetology Section of the "Zoologisches Forschungsmuseum Alexander Koenig" (ZFMK) in Bonn, Germany. Since then, increase of the herpetological collection from less than ca. 9.600 specimens to ca. 100.000. From October 1992 to his retirement Head of the Vertebrate Department and Vice Director of the Forschungsmuseum.

Since winter semester 1980/81 participation in teaching at the "Rheinische Friedrich-Wilhelms-Universität" Bonn; habilitation (thesis on genital morphology in the Sauria) and *venia legendi* received in May 1988. Since then regular teaching and supervision of more than 129 master and 32 doctoral theses, plus 35 theses for state examen. Awarded full professorship ("apl. Professor") April 1996.

Fields of Research. Systematics, ecology and biogeography of amphibians and reptiles, with taxonomic focus on lizards (chameleons, monitor lizards) and its Tertiary and Quaternary predecessors (e.g. lizard amber fossils); genital morphology of squamates. Geographical focus on the western Palearctic Region (founder and editor of "Handbuch der Reptilien und Amphibien Europas", edition of 5 vols. between 1981 and 1999) and West Africa (six larger field excursions to West/Central Africa, each with 1–3 months duration: Spring 1973 Cameroon, winter 1973/74 Cameroon, winter 1975/76 Senegal/Gambia, 1993 Guinea, 1998 Cameroon, 1999 crossing the Sahara in both directions: Morocco, West Sahara, Mauritania, Senegal). In 2002 an extensive educational trip through the eastern half of the USA. Currently 530 sci. publications.

Working group. Members of his ZFMK herpetological working group were/are active in the tropics of Central and South America (Costa Rica, Venezuela, Peru, Bolivia, Chile), Africa (Guinea Bissau, Gambia, Benin, Cameroon, Gabon, Kenya, Zambia) and Madagascar, and of SE Asia (Vietnam, Indonesia).

Societies. September 1979 host and founding member of the "Societas Europaea Herpetologica", which publishes "Amphibia-Reptilia", simultaneously founded at ZFMK, and today the leading journal of its discipline in Europe. Elected for president of the society 1993 in Barcelona, reelected for another 4 years 1997 in Prague.

From 1983 to 1991 Chairman of the "Deutsche Gesellschaft für Herpetologie und Terrarienkunde" (DGHT) which during this period grew from ca. 2000 to over 5000 members, thus becoming the largest association of its discipline in the world. Wolfgang Böhme has the Honorary membership of the DGHT since 1994.

From 2000 to 2002 founding chairman of the working group "Literatur und Geschichte der Herpetologie" of the DGHT with its own periodical "Beiträge zur Literatur und Geschichte der Herpetologie und Terrarienkunde", after two issues, from 2003 onwards, continued as "Sekretär".

From 2001 to 2005 member of the Commission of the "International Committee of Zoological Nomenclature" (ICZN).

From October 1996 to December 2006 President of the "European Association of Zoological Nomenclature" (EAZN).

Elected as 'Honorary foreign member' of the American Society of Ichthyologists and Herpetologists in 2008.

Awarded with the Alexander Koenig Medal in 2010, by the Alexander-Koenig-Gesellschaft, sponsoring society of ZFMK.

Ph. Wagner

Philipp Wagner (Guest Editor)

Bonn, November 2010

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Sharing resources in a tiny Mediterranean island? Comparative diets of *Chalcides ocellatus* and *Podarcis filfolensis* in Lampione

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Abstract. The insular lizard microcommunity inhabiting the Lampione islet (Pelagian islands, S Italy) is constituted by a skink (*Chacides ocellatus*) and a lacertid lizard (*Podarcis filfolensis*). Their diet composition (taxa and sizes) during spring-early summer were analysed based on 131 faecal pellets, which could be individually assigned to a lizard species and sex (only in *P. filfolensis*). The diet of *C. ocellatus* was biased towards hard prey of medium to large sizes (Coleoptera, insect larvae). *Podarcis filfolensis* displayed a more diverse prey spectrum including Formicidae, Coleoptera, insect larvae and minor prey not consumed by the skink, but restricted to the small items; differences between sexes were minimal. Both species were partially herbivorous. Evidence of cannibalism was found for *P. filfolensis* and *C. ocellatus* preyed upon *P. filfolensis*. Pseudocommunity analysis does not support community structure but instead points to convergence in trophic strategies between both species due to insular conditions. Evolutionary history, rather than resource partitioning, seems responsible for the moderate trophic overlaps recorded and even may explain why both species coexist under the harsh conditions of this tiny islet.

Keywords. Diet; *Chacides ocellatus*; *Podarcis filfolensis*; community ecology; islands; Lampione.

INTRODUCTION

For decades, lizards have constituted fruitful model organisms for studies in community ecology, diet being the most studied ecological dimension (see review by Luiselli 2008). Many of the initial and current studies are focused on the most complex assemblages, namely those in tropical or desert areas (Arnold 1984; Pianka 1986; Vitt & Caldwell 1994; Vitt & Carvalho 1995; Vitt & Zani 1998; Vitt et al. 2000; Akani et al. 2002, amongst many others), where environmental stability could allow interspecific relationships promoting detectable community structure (Winemiller & Pianka 1990). In contrast, studies on lizard assemblages inhabiting temperate regions are less abundant (but see Pérez-Mellado 1982; Strijbosch et al. 1989; Pollo & Pérez-Mellado 1991; Carretero & Llorente 1993; Capula & Luiselli 1994; Carretero et al. 2006; Kuranova et al. 2005; Rouag et al. 2007). This is probably because these are composed of less species but also because abiotic restrictions of seasonal climates overcoming the role of species interactions would make community structure less expectable to appear (Barbault 1991). In fact, a recent meta-analysis concluded that lizards of most (80%) communities worldwide do not partition their food resources but are randomly organised in the trophic niche axis (Luiselli 2008). Instead, increasing evidence is demonstrating that the influence of evolutionary history on the lizard trophic traits is stronger than previously thought. Specifically, niche conservatism rather than species interactions accounts for many trophic differences between the community components (Brooks & McLennan 2002; Webb et al. 2002; Vitt et al. 2003; Vitt & Pianka 2005; Mesquita et al. 2007; Espinoza et al. 2008).

Within this context, lizards inhabiting small Mediterranean islands constitute an apparent paradigm of simplicity. On one hand, strong seasonality and impoverished trophic resources impose severe constraints to insular lizards (Pérez-Mellado & Corti 1993), higher than those in adjacent mainland, making lizard communities inhabiting Mediterranean islets extremely poor when compared to those on big islands or on the continent (Mylonas & Valakos 1990).

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On the other hand, the exposition to less potential competitors and predators and subsequent increase in the conspecific density (Carretero 2004, 2006) may open new possibilities for enlarging trophic niche (Pérez-Mellado & Corti 1993; Carretero 2004). Nevertheless, evidence on lacertid lizards indicates that the ecological response to these shifted environmental pressures is not immediate and some evolutionary time is needed to develop profound trophic adaptations (Pérez-Mellado & Corti 1993; Carretero 2004). Literature on the diet of Mediterranean lizards in small islands is abundant but usually focused on a single species (reviewed in Van Damme 1999; Pérez-Mellado & Traveset 1999; Carretero 2004), studies at multispecies level being rare (Nouira 1983).

Here, the diet composition of a microinsular community constituted by two divergent lizard species is analysed during spring-summer considering both inter- and intraspecific variation and compared to other populations of the same species. Moreover, the hypothesis of community structure at the trophic level is specifically tested against the null hypothesis of random trophic overlap.

MATERIAL AND METHODS

Study area

Lampione (35°33'00"N–12°19'11"E) is a small islet located 17 km off the W coast of Lampedusa (Pelagian Islands) and 110 km off Tunisia, in the Channel of Sicily. The area is 0.021 km^2 and the maximum altitude is 36 m a.s.l. From a geological point of view, the islet is composed of dolomitised carbonates belonging to formations of the Tunisian offshore, and its definitive isolation from North Africa was since 18,000 years B.P. (Pasta 2002). The climate is arid, characterised by strong drought periods in summer and by an average annual rainfall lower than 300 mm. The vegetation is mainly dominated by halo-nitrophile perennial shrubs. The occurrence of a large colony of gulls causes a strong level of soil eutrophisation and nutrient imbalances, which allow the expansion of the nitrophile biannual *Malva veneta* Soldano, Banfi & Galasso, 2005 during the late spring on the top of the islet. Lampione is at present-day uninhabited, but late-Roman ruins document an early human presence, though probably only seasonal (Pasta & Masseti 2002). The invertebrate assemblage of the islet reflects several features typical of microinsular and arid environments, namely a low number of species (about 30, excluding flying insects; Lo Cascio 2004, Lo Cascio unpublished), an over-representation of some groups (e.g., five species of Coleoptera Tenebrionidae; Canzoneri 1972; Lo Cascio unpublished), some being found at extremely high densities.

Study lizards

Two lizard species inhabit the islet: the Maltese wall lizard, *Podarcis filfolensis* (Bedriaga, 1876), (Squamata: Lacertidae) and the Ocellated skink, *Chalcides ocellatus* (Forskål, 1775) (Squamata: Scincidae). The first is a genuine insular species endemic to the Maltese Archipelago and two Pelagian islands, Linosa and Lampedusa, where it is said to be introduced in early or recent time (Capula 2006; Lo Cascio & Corti 2008). The Ocellated Skink, *Chalcides ocellatus*, is widely distributed on the Sindian-Mediterranean area and is recorded for all the Pelagian islands (Turrisi & Vaccaro 2006); the origin of the islet population is probably related to the Pleistocene connections between Lampione and the nearby North-African mainland (see Grasso et al. 1985). The first data on the occurrence of such species in Lampione were reported by Lanza & Bruzzone (1961). Population density is extremely high for both species, only for *Podarcis filfolensis* being estimated using standard methods (7500–8000 individuals/ha, see Lo Cascio et al. 2006). From field observations, the ratio of apparent abundance between this species and *Chalcides ocellatus* was 3:1 approximately (Lo Cascio unpublished).

Sampling and lab methods

Field sampling was carried out during several visits in late spring/early summer of 2004 and 2005, when both species show the peak of annual activity (Corti & Lo Cascio 2002). Faecal pellets were obtained from adult *Podarcis filfolensis* and *Chalcides ocellatus*; all the specimens were measured (snout-vent length, SVL) to the nearest 0.1 mm using a digital calliper, sexed (in *P. filfolensis*) and released back in the site of capture. Whereas adult *P. filfolensis* could be easily sexed in the field using sexual secondary characters (Corti & Lo Cascio 2002) and hemipenis eversion, the reduced external differences and the impossibility for analysing of internal cloaca did not allow identifying the sexes of *C. ocellatus* in field (see Badir 1959; Capula & Luiselli 1994).

The faecal contents were examined under stereoscopic microscope (10–40X). Remains were identified to Operational Taxonomy Units (OTUs) approximated here to the order/family level. Item counting was based on cephalic capsules, wings and legs, following the minimum numbers criterion by sample. When possible, prey lengths were obtained measuring the remains with a micrometer eyepiece and calculated by using regression equations (Hódar 1997) and then assigned to classes of 5 mm in length.

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Statistical methods

Three diet descriptors were used: the percentage of pellets containing an OTU (%P), the percentage of numeric abundance of each OTU (%N), and the use index (IU) (Jover 1989); the latter is preferred because combines %N and %P; the importance of a certain OTU in the diet being estimated by calculation of the homogeneity of its consumption throughout all the individual contents (Carretero 2004). Brillouin's index was used to estimate the diet diversity according to Magurran (2004). For a given sample, the average individual diversity (Hi) was obtained by averaging the diversity values of each pellet whereas the (asymptotic) population diversity (Hp) was estimated through jack-knife resampling (Jover 1989, Magurran, 2004), that is, recalculating the total diversity missing out each sample in turn and generating pseudovalues, which are normally distributed. Whereas Hi and Hp have standard errors and allow statistical inference, the total accumulated diversity (Hz) of all pellets is a fixed value only provided for comparing with the literature (Ruiz and Jover 1981).

Overlap between diets was evaluated by means of the Pianka's index (Pianka 1973) applied on the IU values of OTUs and size classes (Carretero et al. 2006) using the Ecosym software (Gotelli & Entsminger 2004). Hypothesis of non-random similarity (Gotelli & Graves 1996) was tested using the RA2 (niche breadth relaxed / zero states retained) and RA3 (niche breadth retained / zero states reshuffled) Monte Carlo randomisation algorithms (Winemiller & Pianka 1990) generating 1000 pseudomatrices considering each OTU equiprobable.

Normality (Lilliefors test) and homoscedasticity (Fisher test) were assured prior to the application of parametric tests. Individual diversity and number of prey per pellet were compared using one-way ANOVA. Population diversity estimations obtained through jack-knife could not be compared using ANOVAs since the software provides only mean±SE and diversity is non-additive (Carretero & Llorente 1993). Instead, t-tests corrected for multiple tests (using False Discovery Rate, FDR, Benjamini & Hochberg 1995) were applied.

RESULTS

Pellets were obtained from 45 *C. ocellatus* and 86 *P. filfolensis* (58 males and 28 females). The SVLs in mm, mean±SE (range) of such specimens were 104.02±2.26 (62.0–140.0) for *C. ocellatus*, 65.45±0.56 (54.0–72.0) for male *P. filfolensis*, and 60.00±0.53 (44.5–67.0) for female *P. filfolensis*, The skinks were, in fact, much bigger than the wall lizards which displayed slight sexual size dimorphism favourable to males (ANOVA $F_{2,128} = 267.58$, $P < 10^{-6}$, Scheffé tests *C. ocellatus-P. filfolensis* males $P < 10^{-6}$, *C. ocellatus-P. filfolensis* females $P < 10^{-6}$, *P. filfolensis* males-females $P = 0.05$).

The number of prey items by pellet (Table 1) was similar between both species and between male and female *P. filfolensis* (ANOVA $F_{2,128} = 0.45$, $P = 0.64$). However, the taxonomic composition of the diet (Table 1) showed substantial interspecific differences, whereas intersexual differences within *P. filfolensis* were minor. Both species consumed important amounts of plant matter (IU = 41.61% in *C. ocellatus* and IU = 18.37% in *P. filfolensis*). Within *P. filfolensis*, males (IU = 22.55%) used this resource more than females (IU = 9.69%). Moreover, *C. ocellatus* also consumed seeds and fruits (IU = 18.31%) but *P. filfolensis* almost did not (IU = 1.24%).

Regarding the prey of animal origin (Table 1), the diet of *C. ocellatus* was strongly biased towards Coleoptera (IU = 24.95%) and only secondarily to insect larvae (IU = 7.79%). In contrast, the animal prey consumed by *P. filfolensis* were more evenly distributed between Formicidae (IU = 26.73%), Coleoptera (IU = 15.08%) and insect larvae (IU = 14.27%) with minimal differences between sexes. Interestingly, the diet of the Maltese wall lizard included some minor prey (Araneae, Pseudoscorpiones, Acarina, Homoptera, Malophaga) that were completely absent from the diet of the Ocellated skink. Overall, animal diet was very similar between male and female *P. filfolensis*, the latter consuming more Araneae and Heteroptera (Table 1). It is worth noting that tails of juvenile *P. filfolensis* were found in adult conspecifics (two in males and two in females) and also in *C. ocellatus* (also two).

Consequently, diet diversity (Table 2) was lower in *C. ocellatus* than in *P. filfolensis*, with no differences between males and females. This was true when considering either individuals (ANOVA $F_{2,128} = 9.93$, $P < 10^{-4}$; Scheffé tests *C. ocellatus* - *P. filfolensis* males $P = 0.0003$, *C. ocellatus* – *P. filfolensis* females $P = 0.0005$, *P. filfolensis* males - *P. filfolensis* females $P = 0.99$) or populations (*C. ocellatus* – *P. filfolensis* males $T_{101} = 4.67$, $P = 5{*}10^{-6}$, $P_{FDR} < 10^{-4}$; *C. ocellatus* – *P. filfolensis* females $T_{71} = 4.82$, $P = 4{*}10^{-6}$, $P_{FDR} < 10^{-4}$; *P. filfolensis* males – *P. filfolensis* females $T_{84} = 1.59$, $P = 0.06$, $P_{FDR} = 0.06$).

As to the size of the items consumed (Table 3), *C. ocellatus* ate bigger prey than *P. filfolensis* but males and females of the latter species did not differ (ANOVA $F_{2,178} = 20.81$, $P < 10^{-6}$, Scheffé tests *C. ocellatus-P. filfolensis* males $P < 10^{-6}$, *C. ocellatus-P. filfolensis* females $P = 5{*}10^{-5}$, *P. filfolensis* males-females $P = 0.94$). The modal size class of *C. ocellatus* was 5–10 mm whereas

P. filfolensis was shifted to the 1-5 mm class. In fact, except in two females, pellets of *P. filfolensis* did not contain items larger than 10 mm. No significant correlation between prey and predator sizes was detected within each group although those *P. filfolensis* females eating the 10–15 mm prey were bigger than the rest (ANOVA $F_{2,35}$ = 5.35, P = 0.009; Scheffé tets: 1–5 mm – 5–10 mm *P* = 0.86, 1–5 mm – 10–15 mm *P* = 0.01, 5–10 mm – 10–15 mm P = 0.01).

Finally, diet overlaps (Table 4) calculated from both taxonomical and size classification of prey were very similar, attaining moderate values between species but high values between male and female *P. filfolensis*. Pseudocommunity analysis at species level revealed that taxonomical overlap was higher than simulated in the RA3 matrix (niche breadth retained, *P* = 0.02) but similar to the RA2 matrix (zero states retained, *P* = 0.50). When considering the three classes (*C. ocellatus*, male and female *P. filfolensis*) none of the two algorithms indicated significant deviations from random. No significant differences were either detected for the size overlap.

DISCUSSION

Differences in lizard diet arise from multiple factors including anatomy, sex, reproductive state, body condition, experience, prey availability, predation pressure, competition and evolutionary history (Schoener 1974; Dunham 1980; Pianka 1986; Losos 1992; Vitt & Zani 1998; Vitt et al. 1999; Perry & Pianka 1999; Pitt & Ritchie 2002; Carretero 2004). In Lampione, the manifest size differences between both species constitute the most obvious constraint for the prey they consume. Within species, prey sizes tend to follow a logarithmic distribution, small individuals simply not been able to consume the biggest items of the prey spectrum of the large individuals (Pianka 1986). However, between species this pattern can be altered if drastic divergence in anatomy or foraging tactics occurs (Carretero 2004). This seems to be the case, since *C. ocellatus* not only consumed large prey inaccessible for *P. filfolensis* as expected, but also kept the same number of prey items but biased to medium sizes. This result suggests that both species may follow different foraging strategies (Perry & Pianka 1999). In fact, *C. ocellatus* is described a semi-fossorial, sit-and-wait forager in plant litter or under stones (Arnold 1984; Capula & Luiselli 1994; Kalboussi & Nouira 2004; Lo Cascio et al. 2008) whereas *P. filfolensis* as most lacertids actively forages on the surface (Corti & Lo Cascio 2002; Bombi et al. 2005; Lo Cascio et al. 2006). Nevertheless, there is also evidence for anatomical constraints, since ocellated skinks consumed more hard prey (Coleoptera) than the wall lizards. In lacertids, large species tend to consume more Coleoptera (Carretero et al. 2006) and there is experimental evidence for inter- and intraspecific differences in bite force for prey crashing associated with the jaw muscle mass (Herrel et al. 1999, 2001). Nonetheless, sexually dimorphic lacertid heads, as intersexual differences in bite force, primarily derive from sexual selection (Herrel et al. 1999; Kaliontzopoulou et al. 2007), and dietary shifts (minimal in *P. filfolensis*) should be interpreted as a by-product.

While divergent anatomy, foraging tactics and habitat use between both species accounted for a substantial part of the interspecific variation found, comparison with other populations indicates that other factors modified the taxonomic composition of their diets. As other insular lacertids in the Mediterranean (Pérez-Mellado & Corti 1993; Carretero et al. 2001; Corti et al. 2008), *P. filfolensis* consumed great amounts of ants not only in Lampione but also in Linosa (Sorci 1990; Bombi et al. 2005) and Lampedusa (Lo Cascio & Corti 2008). Since only *Podarcis* populations inhabiting ancient Mediterranean islands (i.e. Balearics, Mylos) are myrmecophagous, this has been interpreted as a result of long term evolution in insularity (Pérez-Mellado & Corti 1993; Carretero 2004). The decrease in predation pressure, the scarcity of alternative resources, together with the gregarious behaviour and seasonal stability of this prey may compensate for its low profitability and noxiousness (Carretero 2004). Apparently, *C. ocellatus* has not been able to follow a similar strategy since neither continental nor insular populations are myrmecophagous (Capula & Luiselli 1994; Kalbousssi 2004; Lo Cascio & Corti 2008). Whether this is due to evolutionary constraints or to recent colonisation of Lampione currently remains under debate.

Cannibalism and, in general, saurophagy seem also to increase in insular conditions due to the scarce resources and high lizard densities (Pérez-Mellado & Corti 1993; Carretero et al. 2001) as is the case of *P. filfolensis* and *C. ocellatus* (Scalera et al. 2004; Lo Cascio et al. 2006). However, the predation of *P. filfolensis* by *C. ocellatus* constitutes not only an additional food source but also an instance of direct, asymmetric interaction between both species (Chase et al. 2002).

As in the case of the ants, plants are also low profitable matter and their consumption seems to be restricted to old insular lacertid lineages which have developed behavioural and anatomical adaptations for herbivory (Pérez-Mellado & Corti 1993; Carretero 2004). Both *P. filfolensis* and *C. ocellatus* were partially herbivorous in Lampione. However, other populations of *P. filfolensis* studied also consumed substantial amounts of seeds, fruits and other plant remains (Sorci 1990; Bombi et al. 2005; Lo Cascio & Corti 2008) and even seed dispersal for some plant species has been described in Linosa (Fici & Lo Valvo 2004). This suggests niche conservatism for herbivory in this species. In contrast, herbivory seems to be rare in *C. ocellatus*. Only two other microinsular populations, on Lampedusa and the Conigli islet (Lo Cascio & Corti 2008; Lo Cascio et al. 2008), were partially herbivorous, whereas, no or almost no plant remains were found in the populations from Sardinia (Capula & Luiselli 1994) and Tunisia (Kalboussi & Nouira 2004). Nevertheless, even continental ocellated skinks accept fruits in captivity (Schleich et al. 1996) suggesting certain exaptation for herbivory in this species. Comparing the *C. ocellatus* population from Lampione with those from the other Pelagian islands (Lo Cascio & Corti 2008; Lo Cascio et al. 2008), there is an apparent trend for increasing the degree of herbivory with isolation and for decreasing it with island area.

The analysis of trophic diversity indicates that *P. filfolensis* is more euryphagous than *C. ocellatus*, with minimal intraspecific variation in the first. Remarkably, for both species, trophic diversity was much higher in populations than in individuals, indicating strong interindividual variation typical of generalist predators (Carretero et al. 2006). In fact, *C. ocellatus* displayed even stronger differences (4x) than *P. filfolensis* (3x), which is accordance with its sit-and-wait trend.

Finally, niche overlap summarises the trophic traits of the community previously exposed. Coincidence between taxonomical and size overlaps and higher values between species than within species indicate that intrinsical morphological constraints constitute the main force for the organisation of this microinsular community. Pseudocommunity analysis does not support community structure but instead points to enlarged, more overlapped trophic niches.

When compared to other conspecific populations, convergence in trophic strategies (herbivory, saurofagy) between both species due to insular conditions seems the more feasible hypothesis for explaining these results. Moreover, evolutionary history at both deep (foraging strategies, Vitt & Pianka 2005) and shallow (recent or ancient insular colonisation, see above) levels seems, rather than resource partitioning, responsible for the moderate trophic overlaps recorded and even may explain why both species coexist under the harsh conditions of this tiny islet. Nevertheless, coincidence of trophic overlap between two species with the direct predation of one on the other merits further analyses (see also Castilla 1995).

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Appendix

Table 1. Descriptors of the taxonomic composition of the diet for *Chalcides ocellatus* and *Podarcis filfolensis* from Lampione island. OTU: Operational taxonomical unit, %P: percentage of presence; %N: percentage of numerical abundance; IU: Resource use index: – not consumed; 0.00: consumed but index value next to zero.

	Chalcides ocellatus total			*Podarcis filfolensis* total			*Podarcis filfolensis* males			*Podarcis filfolensis* females		
OTU	%P	%N	IU	%P	%N	IU	%P	%N	IU	%P	%N	IU
Gastropoda	9.09	1.28	0.65	2.33	0.39	0.09	–	–	–	7.14	1.16	0.42
Isopoda	9.09	1.28	0.65	11.63	1.94	1.47	10.34	1.74	1.13	14.29	2.33	1.70
Araneae	–	–	–	12.79	2.13	1.68	5.17	0.87	0.35	28.57	4.65	5.10
Pseudoscorpiones	–	–	–	12.79	2.71	2.04	15.52	2.91	2.24	7.14	2.33	0.85
Acarina	–	–	–	2.33	0.39	0.09	3.45	0.58	0.15	–	–	–
Diptera	15.15	2.55	1.79	24.42	6.01	5.66	27.59	6.98	6.51	17.86	4.07	3.20
Coleoptera	66.67	18.30	24.95	55.81	12.40	15.08	56.90	12.21	14.98	53.57	12.79	16.48
Hymenoptera	–	–	–	25.58	7.56	6.95	27.59	7.27	6.41	21.43	8.14	7.04
Formicidae	18.18	4.26	3.19	60.47	23.45	26.73	58.62	22.38	25.18	64.29	25.58	31.15
Homoptera	–	–	–	6.98	1.74	0.97	10.34	2.62	1.60	–	–	–
Heteroptera	6.06	0.85	0.27	17.44	3.49	2.90	13.79	2.33	1.75	25.00	5.81	5.25
Mallophaga	–	–	–	9.30	1.55	1.06	10.34	1.74	1.13	7.14	1.16	0.42
insect larvae	30.30	8.51	7.79	37.21	14.15	14.27	34.48	15.70	14.93	42.86	11.05	13.26
Arth ind.	9.09	1.70	0.78	9.30	1.55	1.06	5.17	0.87	0.35	17.86	2.91	2.47
Squamata	3.03	0.43	0.00	4.65	0.78	0.35	3.45	0.58	0.15	7.14	1.16	0.42
seeds, fruits	21.21	25.53	18.31	6.98	3.10	1.24	6.90	1.16	0.59	7.14	6.98	2.55
other plant matter	54.55	35.32	41.61	45.35	16.67	18.37	53.45	20.06	22.55	28.57	9.88	9.69
Total (mean±SE)	45 pellets, 235 items 5.91±0.83 items/pellet			86 pellets, 516 items 5.19±0.34 items/pellet			58 pellets, 344 items 5.16±0.38 items/pellet			28 pellets, 178 items 5.25±0.70 items/pellet		

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Table 2. Diet diversities of *Chalcides ocellatus* and *Podarcis filfolensis* from Lampione island. Numbers indicate mean±SE. Hi: individual diversity; Hp: population diversity; Hz: total accumulated diversity; all using Brillouin's index.

Species (class)	N	Hi	Hp	Hz
Chalcides ocellatus (total)	45	0.61±0.03	2.57±0.11	2.44
Podarcis filfolensis (total)	86	0.98±0.02	3.33±0.08	3.22
Podarcis filfolensis (males)	58	0.98±0.03	3.19±0.08	3.05
Podarcis filfolensis (females)	28	0.98±0.06	3.43±0.14	3.17

Table 3. Descriptors of the prey size composition of the diet for *Chalcides ocellatus* and *Podarcis filfolensis* from Lampione island. OTU: Operational taxonomical unit, %P: percentage of presence; %N: percentage of numerical abundance; IU: Resource use index: – not consumed; 0.00: consumed but index value next to zero.

	Chalcides ocellatus total			*Podarcis filfolensis* total			*Podarcis filfolensis* males			*Podarcis filfolensis* females		
OTU	%P	%N	IU	%P	%N	IU	%P	%N	IU	%P	%N	IU
0–5 mm	32.14	24.62	19.09	80.00	67.24	68.92	73.68	64.10	64.41	100.00	73.68	78.66
5–10 mm	85.71	58.46	69.63	84.00	31.03	31.08	84.21	35.90	35.59	83.33	21.05	21.34
10–15 mm	17.86	7.69	5.31	4.00	1.72	0.00	–	–	–	16.67	5.26	0.00
> 15 mm	17.86	9.23	5.96	–	–	–	–	–	–	–	–	–
Total (mean±SE)	65 (of 235) items measured 7.42±0.51 mm			116 (of 516) items measured 4.22±0.24 mm			78 (of 344) items measured 4.29±0.27 mm			38 (of 178) items measured 4.08±0.47 mm		

Table 4. Diet overlaps (Pianka's index) between the lizard species and classes from Lampione island considering the taxonomical and size composition of the prey consumed.

	taxonomical overlap	size overlap
C. ocellatus (total) – *P. filfolensis* (total)	0.54	0.63
C. ocellatus (total) – *P. filfolensis* (males)	0.54	0.64
C. ocellatus (total) – *P. filfolensis* (females)	0.53	0.50
P. filfolensis (males) – *P. filfolensis* (females)	0.97	0.97

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Evolutionary reproductive morphology of amphibians: an overview

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Abstract. Reproduction is a crucial trait in the life history of any organism, and vertebrates, whether aquatic or terrestrial, have evolved an extraordinary diversity of reproductive strategies and morphologies. Among tetrapods, the diversity of reproductive modes is exceptionally high in amphibians, who also show multiple trends towards terrestrialisation and internal fertilisation. Herein we give a brief overview of the diversity of amphibian reproductive morphology, with a special emphasis on the cloaca, for all three major lineages, i.e., anurans, urodeles and caecilians.

Key words. Reproduction, genital morphology, Amphibia.

INTRODUCTION

Reproduction is a crucial trait in the life history of any organism and scientists have been intrigued and challenged by this event, and the structures associated with it, ever since the days of Darwin (1871). Both aquatic and terrestrial vertebrates have evolved an extraordinary diversity of reproductive strategies and morphologies, including varieties of oviparity and viviparity (Meisenheimer 1921; Lombardi 1998). Among tetrapods, the diversity of reproductive modes is exceptionally high in amphibians. In this group, we also see multiple trends towards terrestrialisation and internal fertilisation (e.g. Haddad & Prado 2005). Reproductive modes such as viviparity have evolved independently in all three lineages of modern amphibians (e.g. Noble 1927; Wake & Dickie 1998; Wells 2007). Herein we interpret a reproductive mode as a combination of several reproductive traits, including oviposition site, clutch characteristics, stage and size of hatchling, and type of parental care (sensu Salthe 1969).

Internal fertilization is a precondition for viviparity (Wourms & Lombardi 1992; Böhme & Ziegler 2008). It is associated with different strategies of sperm transfer, which have evolved within all three amphibian orders, ranging from cloacal apposition in anurans to a true copula via a male intromittent organ in caecilians (Sever et al. 2001; Kupfer et al. 2006). Like most other tetrapods, amphibians have a cloaca, a chamber that receives products from the kidneys, the intestine and the gonads, and opens to the outside through a cloacal opening or vent (Kardong 2006).

Below we review the diversity of amphibian cloacal morphologies involved in ensuring a secure direct sperm transfer and internal fertilization among anurans, urodeles and caecilians.

REPRODUCTIVE MORPHOLOGY OF AMPHIBIANS

Anura

The majority of anurans, currently including almost 6000 species (AmphibiaWeb 2010), practice external fertilization, and thus have no special male cloacal arrangements facilitating direct sperm transfer (recently summarised by Wells 2007). During copulation, males grasp females firmly with their forearms (termed amplexus). In most cases, sperm is directly released on the eggs protruding from the female cloaca, but in some cases fertilisation takes place without amplexus (e.g. Crump 1974; Kunte 2004). Internal fertilisation is rare among anurans, and mostly connected to viviparity or other complex parental care mechanisms (e.g. Wake 1993; Beck 1998).

Exceptionally, the phylogenetically basal tailed frogs *Ascaphus truei* and *A. montanus* are the only anurans known to have evolved a true intromittent organ in males (see Figs 1A–B). During courtship they practise a combination of amplexus and copulation called “copulexus” (see Sever et al. 2001; Stephenson & Verrell 2003). The so-called

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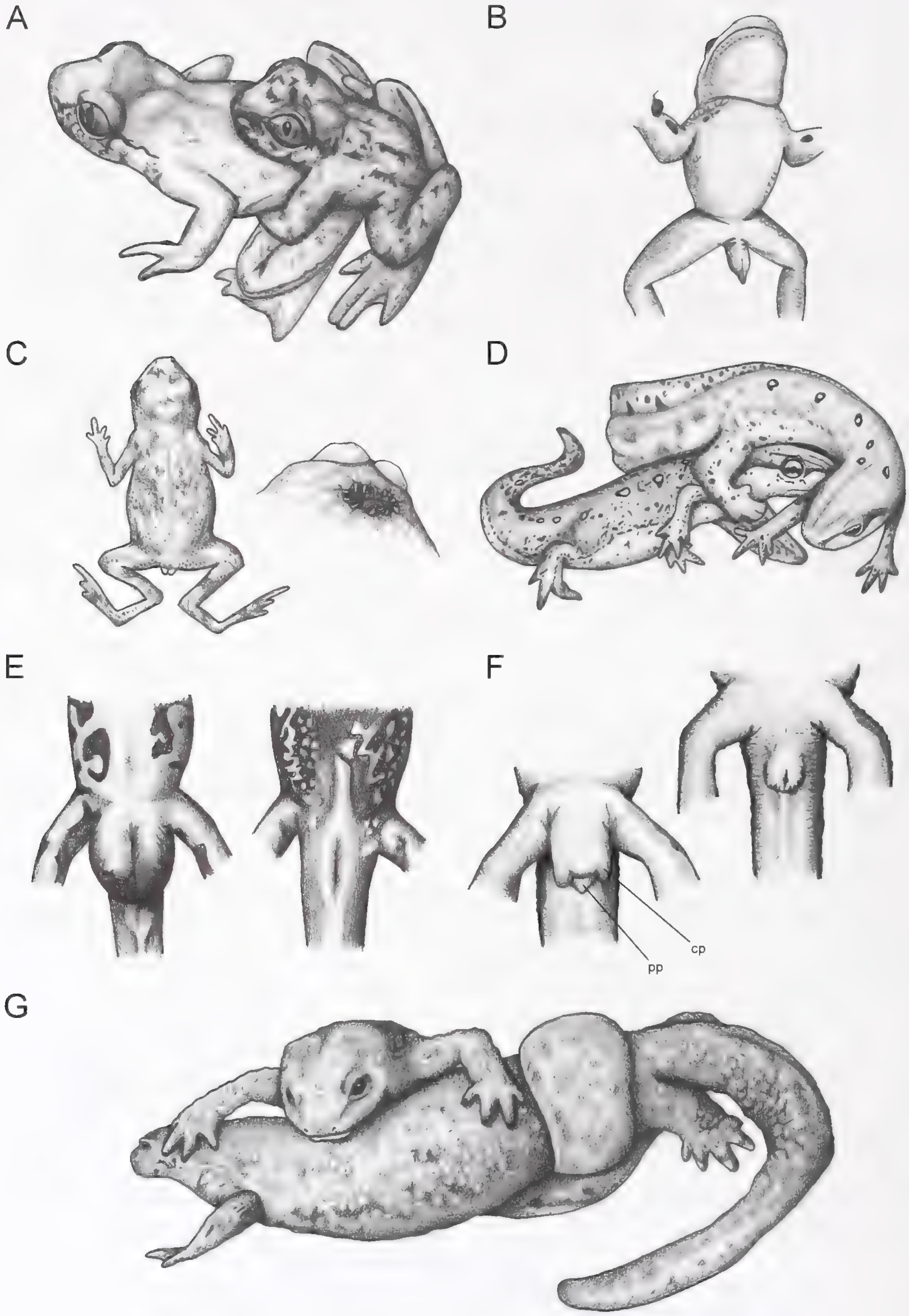

Fig. 1. Reproductive morphology of anurans and salamanders. (A) Inguinal amplexus ("copulexus") of *Ascaphus truei*. (B) male *Ascaphus truei*. The "tail", a cloacal extension, can be inserted into the cloaca of the female during amplexus, ventrolateral view. (C) male *Mertensophryne micranotis* (Anura: Bufonidae), left, dorsal view and its cloaca, right, caudal view (after Grandison 1980). (D) cephalic amplexus of *Notophthalmus viridescens* (Urodela: Salamandridae). The male grasps the females's neck whilst fanning pheromones towards her nostrils. (E) cloacal region of lentic breeding *Cynops pyrrhogaster* (Urodela: Salamandridae). The male's cloaca (left) is heavily swollen compared to that of the female (right). (F) cloacal region of lotic breeding *Euproctus montanus* (Urodela: Salamandridae, after Brizzi et al. 1995). Males (left) possess a cloacal protuberance (cp) which bears a protusible pseudopenis (pp), whereas the female cloaca is slightly conical shaped and its opening is located ventrally (right). (G) amplecting pair of *Calotriton arnoldi* (Urodela: Salamandridae). The male grasps the female's trunk with his tail.

"tail" resembles the posteriorly extended cloaca, proximately attended by Nobelian rods and strengthened by vascularized tissue that is engorged with blood during copulation. This gives the ventral cloacal surface a pinkish colour (Noble & Putnam 1931; Duellman & Trueb 1994). To insert the posterior pointing "tail" into the female vent, the male first flexes his pelvis at a right angle to the vertebral column. Contraction of the paired Musculi compressores cloacae (Duellman & Trueb 1994) bend the intromittent organ ventrally, with the male vent pointing anteriorly (Slater 1931). Keratinised spines are present within the male cloacal orifice, but whether they function to enhance the attachment of the male to the female remains unclear (Noble & Putnam 1931; Metter 1964).

Additionally, internal fertilisation including an amplexus and cloacal apposition occurs in a few anurans, such as several species of viviparous African dwarf toads *Nectophrynoides* (Wake 1980; Wake & Dickie 1998) and *Nimbaphrynoides* (Sandberger et al. 2010), and in two species of Caribbean *Eleutherodactylus*, the viviparous *E. jasperi* (Dewry & Kirkland 1976; Wake 1978) and the oviparous-direct developing *E. coqui* (Townsend et al. 1981). Mating has only been observed in couples of *E. coqui* in a special amplectic position called reverse hind leg clasp, that is initiated by the female (Townsend & Stewart 1986). Males do not clasp, and the female rests her hind legs on top of the male´s legs. This behaviour might be correlated with terrestrial reproduction and internal fertilization. It is also thought to be present in the viviparous *E. jasperi* but has not yet been observed (Wake 1978). Within the African Bufonidae, all species of *Nectophrynoides* (and also *Altiphrynoides malcolmi* and *Nimbaphrynoides occidentalis*, former members of *Nectophrynoides,* see Frost et al. 2006) practice internal fertilization. *Altiphrynoides* and *Nimbaphrynoides* both show a dimorphism of the male and female vent, and an inguinal amplexus in a unique belly-to-belly position has been reported as well (Grandison 1978).

As in the internally fertilising *Ascaphus* ssp., males of the East African toad *Mertensophryne micranotis* (Bufonidae) exhibit modifications of the cloacal region (Duellman & Trueb 1994). They have small conical spines around the rim of the vent and at the entrance to the cloacal tube restricted to the ridges of the puckered vent (Grandison 1980, see also Fig 1C). Males and females keep a very tight cloacal contact during mating. Although the cloacal spines play a role to ensure a close apposition of the vents, to secure internal fertilisation, there is no evidence for a direct interlocking mechanism in the furrows of the female vent (Grandison & Ashe 1983).

Another potential record of internal fertilisation is provided for the neotropical Pumpkin Toadlet *Brachycephalus ephippium* (Pombal et al. 1994). During mating, males shift from an inguinal to an axillary amplexus to optimally allow positioning of the vents, and thus maximize fertilization of the relatively large eggs (5.1 to 5.3 mm). A further record of viviparity in fanged frogs (*Limnonectes* spec.) from Sulawesi probably also involves internal fertilisation(Emerson 2001).

It can be hypothesised that (1) many terrestrially breeding species with large direct-developing clutches are internal fertilizers and (2) if additional viviparous species are encountered they will also show internal fertilisation. Thus, internal fertilisation and viviparity in anurans might be more widespread than currently recognized (see also Wake 1978).

Data on the reproductive biology, including the mating behaviour, of many species is still lacking (Duellman & Trueb, 1994; Wells 2007). Life history data from around 23 % of the currently known species is missing, as listed in the data deficient category of the IUCN (Stuart et al. 2008).

Urodela

The majority of the 590 species of urodeles exhibit internal fertilization, whilst only males of the basal families Hynobiidae, Cryptobranchidae, and presumably Sirenidae, fertilise eggs externally (summarised in Duellmann & Trueb 1994; Wells 2007). The complex and elaborate courtship behavior of most salamanders includes the deposition of a spermatophore by the male, which is subsequently received by the female. A true intromittent organ in salamanders is lacking, although direct sperm transfer can be found in one species – the Corsican brook newt *Euproctus montanus*, a lotic breeding endemic of the island of Corsica. The cloaca of the male brook newt resembles a conical protuberance (Fig 1F). The cloacal chamber hosts a "pseudopenis", a broad conspicuous papilla, which can be evaginated during mating (Brizzi et al. 1995; Carranza & Amat 2005). The male grasps the female during amplexus, holding her tail with his jaws and wrapping his tail around her trunk, whilst his backward projecting cloaca is positioned close to that of the female. A deep groove along the ventral surface of the pseudopenis, which is aligned with the cloacal tube, guarantees a guided, unidirectional flux of cloacal products. Thus, sperm mixed with secretory products is transferred directly into the female's cloaca. The Salamandroidea that practice internal fertilization possess a distinct set of male cloacal glands necessary for spermatophore production (Sever 2002). The glands are hormonally controlled and hypertrophied during the breeding season, often causing a sexual dimorphism in cloacal shape. However, in *Euproc-*

tus montanus, cloacal glands are reduced or partly lacking (Brizzi et al. 1995; Sever 2002). Males of six salamandrid genera possess a so-called "pseudopenis", a projection of the dorsal roof which nearly fills the entire anterior chamber of the cloaca. It is involved in shaping and expulsion of the spermatophore (Halliday 1998), but cannot be everted as in the Corsican brook newt (Brizzi et al. 1995; Carranza & Amat 2005).

Sexes of most species, regardless of the mode of fertilisation, show a sexual dimorphism in cloacal shape (Figs 1E–F). Usually, the male cloaca appears larger and more swollen than the female one. This is caused by the activity of the glands mentioned above (see also Sever 2002). Species that breed in the water and show elaborate courtship dances or walks, such as some members of the family Salamandridae, produce courtship pheromones, which are fanned towards the female using the tail. Salamanders that mate terrestrially also use courtship pheromones secreted from specialised glands to attract females. Pheromone-producing cloacal glands are therefore highly influenced by sexual selection (e.g. Sever 2002; Houck et al. 2008). Usually, female cloacae are less prominent, but they may also possess up to three types of cloacal glands in Salamandroidea, mainly accounting for sperm storage (spermathecae), a unique feature among vertebrates (Sever 1994). Females may retain and mix viable spermatozoa from multiple matings in the spermathecae for longer periods (e.g. Steinfartz et al. 2006). Female *Eurycea* fertilise eggs from stored sperm up to eight months after insemination, female *Notophthalmus viridescens* effectively store sperm for up to six months, and female *Salamandra salamandra* are reported to store sperm for up to two years (Sever et al. 1996; Stebbins & Cohen 1997; Sever & Brizzi 1998).

Additionally, the shape of female cloacae can be adapted to a specific substrate for oviposition and type of water body. Females of stream-breeding species, such as *Calotriton asper*, sometimes have a conically shaped cloaca for egg deposition and safe attachment between stones and in crevices (e.g. Carranza & Amat 2005).

Lotic breeders such as *Calotriton* ssp. often engage in an amplexus directly transferring the spermatophore into the female cloaca (Fig 1G). It ensures direct and rapid spermatophore uptake, and thus reduces energy wasting, which can hardly be avoided during aquatic breeding where the male and the female often have no physical contact. Breeding patterns including an amplexus are common in salamandrids. Multiple ways of female capture are known, such as the cephalic capture of *Notophthalmus* ssp. (see Fig 1D), the dorsal capture of *Taricha*, or the ventral capture performed by fire salamanders (Stebbins & Cohen 1997). The mating amplexus may last up to several hours, depending on the species. Salamanders of the family Ambystomatidae mate in the water, and the males guide females to spermatophore-uptake using a "tail-nudging-walk", except in *Ambystoma gracile*, *A. laterale*, *A. jeffersonarium* and *A. macrodactylum*, which capture females in an amplexus (Duellmann & Trueb 1994; Verrell & Krenz 1998). In contrast, some plethodontids perform a unique "tail-straddling-walk" behaviour (e.g. Arnold 1977).

Gymnophiona

In contrast to all salamanders (with the exception of *Euproctus montanus*) and frogs (with the exception of *Ascaphus* ssp.), the male caecilian cloaca is evertible through the vent and operates as an intromittent organ or phallus, a unique structure among tetrapods (Tonutti 1931, see also Fig 2A). Presumably all ca. 190 caecilian species (oviparous and viviparous) practice internal fertilisation with the help of the phallodeum (Tonutti 1931; Wake 1972; Gower & Wilkinson 2002), which is inserted into the female vent during copulation (e.g. Kupfer et al. 2006a).

The caecilian vent is simply surrounded by several folds, which are variably arranged among the groups and display sexual dimorphism in some species, such as members of the Typhlonectidae (e.g. Taylor 1968; Kupfer 2007). In contrast, the cloaca is highly complex and diverse. The male caecilian cloaca is an elongated tube divided into two distinct chambers. The cranial urodeum is rather simply built, bearing longitudinal ridges, and connects to the intestine and the urogenital ducts, which enter after performing a U-bend (Sawaya 1942; Gower & Wilkinson 2002). An extraordinary feature is the presence of Müllerian ducts, which become glandular during reproductive activity, and secrete a fluid containing lipids and sugars necessary for sperm motility (e.g. Wake 1981). The caudal phallodeum is more broadly built and the inner structure is very different. The ridges are arranged in a more complex pattern (running transversely). In adults it is often equipped with tuberosities or crests, which give the phallodeum a characteristic morphology and gives rise to an extraordinary variation in shape (Wiedersheim 1879; Tonutti 1931, 1933; Wake 1972; Exbrayat 1991; Gower & Wilkinson 2002, see also Fig 2), that is impotant for caecilian systematics (Müller et al. 2005). East-African scolecomorphid caecilians even have cartilaginous spicules (Wake 1998). In many species, pouchy dorsolateral appendixes – so called "blind sacs" – extend anterior to the phallodeum. During eversion, the luminal surface of the phallodeum represents the outer structure of the phallus, with the urodeum lying in-between (see Tonutti 1931; Gower & Wilkinson 2002, see also Fig. C right).

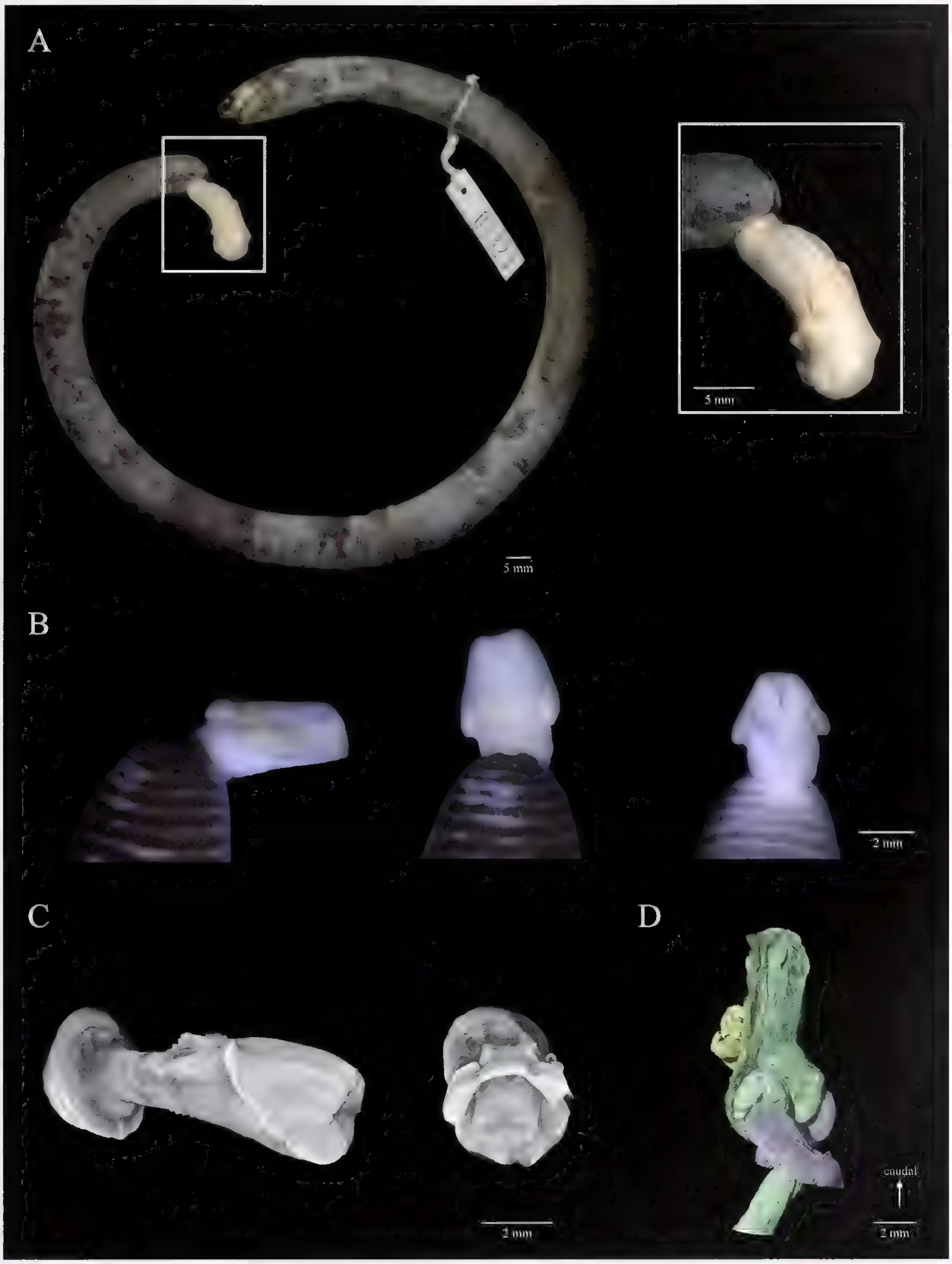

Fig. 2. Genital morphology of caecilian amphibians. (A) male *Chthonerpeton indistincum* (Gymnophiona: Typhlonectidae) showing an everted phallus, MHNM 09323, right – detail. (B) *Geotrypetes seraphini* (Gymnophiona: Caeciliidae), lateral (left), dorsal (central) and ventral (right) view of the everted phallus, AK 01149. (C) *Typhlonectes natans* (Gymnophiona: Typhlonectidae), SRμCT-Scan of the everted phallus. Right – virtual clipping, frontal view. (D) SRμCT-Scan of female cloaca (*Ichthyophis* cf. *kohtaoensis*). Dorsolateral view, virtual cut of cloacal sheath, cranial part and blind sacs, green - cloaca, violet – oviducts, yellow – bladder. Abbreviations: MHNM = Museo Nacional de Historia Natural Montevideo Uruguay, AK = Alexander Kupfer collection.

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To retract the cloaca within the body after copulation, caecilians possess a specific muscle (musculus retractor cloacae), which is also found in some females (Wilkinson 1990).

The female cloaca of caecilians has received little attention (e.g. *Hypogeophis rostratus* Tonutti 1931; *Typhlonectes compressicauda*, Exbrayat 2006), the only dedicated morphological study was presented by Wake (1972), proposing a functional association between the specific male and female morphologies. The female cloaca is supposed to be non-eversible (Wilkinson 1990), therefore displaying a different morphology. Generally it is shorter than in males, and the urogenital ducts lack a copulatory loop (see Fig. 2D). There is also evidence for a bisection of the female cloaca (Exbrayat 1991; Kühnel et al. submitted). The cranial chamber is homologous to the male urodeum. The caudal chamber is marked by a different arrangement of longitudinal cloacal folds mostly lacking tuberosities, and therefore easily recognised. Nothing is at present known about how far the male phallus inserts into the female cloaca, and if special structures corresponding to the male ornamentation are present, helping in fixation during copulation.

Copulations in caecilians have rarely been observed. Data are available for two aquatic/semiaquatic species, the typhlonectids *Typhlonectes compressicauda* and *Chthonerpeton indistinctum*. Pairs of *C. indistinctum* copulated for betwen 30 minutes and 5 hours (Barrio 1969) and those of *T. compressicauda* for between 75 minutes and 3 hours (Murphy et al. 1977; Billo et al. 1985). Observations on copulations in terrestrial caecilians have, to the best of our knowledge, only been presented for the Indian ichthyophiid *Ichthyophis beddomei* (Bhatta 1999) and *Ichthyophis* cf. *kohtaoensis* (Kupfer et al. 2006a). Bhatta reports on a copulation lasting for about 40 or 45 minutes, an observation fitting well with the duration time of about 45 minutes that was observed in *Ichthyophis* cf. *kohtaoensis* (Kupfer et al. 2006a).

Caecilians show a remarkable diversity of reproductive modes associated with parental care (e.g. Wake 1977; Himstedt 1996; Wilkinson & Nussbaum 1998). Oviparous caecilians guarding egg clutches in terrestrial chambers (e.g. Sarasin & Sarasin 1887–1890) either have the presumed ancestral amphibian life cycle with aquatic larvae, or show direct development of juveniles with no aquatic larval stage (e.g. Brauer 1897). Females of viviparous species retain fertilised eggs. Embryogenesis is completed within the oviducts, and after hatching the foetuses feed mainly intrauterinely on the hypertrophied oviductal lining (e.g. Parker 1956; Welsch et al. 1977). After a long gestation period, the females give birth to fully metamorphosed, precocial young with the adult-type morphology (e.g. Billo et al. 1985; Exbrayat & Delsol 1985). Recently, a novel form of parental investment, maternal dermatotrophy, a.k.a. skin feeding, where altricial young feed externally on the mother´s hyperthrophied skin, has been described (Kupfer et al. 2006b; Wilkinson et al. 2008).

SUMMARY AND PERSPECTIVES

In addition to their remarkable diversity of reproductive modes, amphibians also show large variation in their reproductive morphology. Many morphological peculiarities are related to the evolution of internal fertilisation, and ultimately to viviparity. In relation to fertilisation and sperm transfer, different strategies have evolved within the three amphibian orders, ranging from cloacal apposition in anurans to a true copula via a highly complex male intromittent organ in caecilians. Amphibians offer a prime system for comparative studies of evolutionary reproductive biology. Research on the reproductive or genital morphology should include modern methodology, such as 3D reconstruction and soft tissue synchrotron radiation based X-ray microtomography (SRµCT, see Fig. 2 C–D). Because amphibian diversity is steadily increasing (although at the same time many species are declining or even going extinct) we envisage that many more unexpected reproductive strategies and morphologies remain to be discovered.

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Updated checklist of the living monitor lizards of the world (Squamata: Varanidae)

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Abstract. We provide an update of Böhme's (2003) checklist of the living monitor lizards of the world. Since this contribution, ten new species and one new subspecies have been described. Ten of these taxa were described from the islands of the Indo-Australian Archipelago. One *Soterosaurus* taxon (*macromaculatus*) was revalidated to subspecies status, whereas the younger melanistic taxon *komaini* was synonymized with the former. In addition, five taxa (*beccarii*, *cumingi*, *marmoratus*, *nuchalis*, and *togianus*), that were formerly treated as subspecies, were re-elevated to species rank resulting in 73 extant species (including 21 subspecies). This represents a 20% increase of the world's varanid diversity since 2003. In addition, ongoing taxonomic studies on *V. spinulosus* from the Solomon Islands (formerly a member of the *V. indicus* species group) indicate that this species most likely represents a new subgenus. Therefore, this taxon is currently treated incertae sedis. In sum, taxonomic research in monitor lizards remains incomplete. Further studies must be initiated to fully understand diversity and distribution of these CITES-listed lizards next to implications for sustainable conservation measures.

Key words: Reptilia, *Varanus*, *Philippinosaurus*, *Soterosaurus*, *Euprepiosaurus*, *Odatria*, checklist.

INTRODUCTION

Monitor lizards are among the largest living squamates of the world. They inhabit Africa, the Arabian Peninsula, South and Southeast Asia as well as the Indo-Australian Archipelago including Australia and several Pacific island groups. Due to their often large body size and ecological role as top predators in most environments they inhabit, monitor lizards have always been a small reptile group comparable to large placental carnivores (Sweet & Pianka 2007). Nevertheless, the diversity of monitor lizards has been underestimated for many decades.

One of the latest comprehensive listings of all extant monitor lizards was published by Böhme (2003), who listed 58 different species and 28 subspecies. This checklist was prepared at the request of the Nomenclature Committee of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), because of the increase in monitor lizard diversity in the early 1990s. This caused considerable confusion within trade records, which made communication about these economically important lizards in the CITES domain rather difficult. Therefore, Böhme's (2003) checklist was adopted as the standard reference for the Varanidae by the 12th Conference of the Parties to CITES in November 2002.

The need for an updated list only seven years after the last synopsis by Böhme (2003) derives from ongoing descriptions of new species. This is partly due to the fact, that the understanding of monitor lizards, their systematics, and the underlying concepts have been refined in recent years (e.g. Koch et al. 2009). In addition, the taxonomic status of several nominal taxa has changed. This involves either subspecies elevated to species rank or the subgeneric allocation of species. Also, knowledge of distribution ranges of some rare monitor lizard species has been advanced by the examination of new voucher specimens and investigations in the field.

Next to taxonomic and phylogenetic studies on the Varanidae, those focusing on conservation particularly of the Indo-Australian realm remain scarce. A summary of threats monitor lizards are exposed to in this region, cur-

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rent conservation studies and measures in place, and the conservation status of all Indo-Australian species will be outlined in detail elsewhere.

METHODS

In the present paper, we compiled all monitor lizard taxa that were published after Böhme (2003). This includes also such names where the taxonomic status has changed. We basically follow the format of this author, which has earlier been used by Mertens (1963).

The synonymy list of each taxon starts with the original citation and is then arranged chronologically with the source of the respective name and its type locality. Chresonyms are generally not included with the exception of names with a changed taxonomic status exemplified by subspecies names, that were elevated to species level or when a new species is separated from a long recognized species. In these cases, the taxon name and the author(s) are separated by a "–". In addition, type specimens for valid taxa are provided, if available. Collection acronyms are as follows: BMNH = British Museum of Natural History, London, UK; KU = Kansas University, Museum of Natural History, Lawrence, USA; MNHN = Muséum national d'Histoire naturelle, Paris, France; MSNG = Museo Civico die Storia Naturale di Genova Giacomo Doria, Genova, Italy; MZB = Museum Zoologicum Bogoriense, Bogor, Indonesia; NMW = Naturhistorisches Museum Wien, Vienna, Austria; PNM = Philippine National Museum, Manila, Philippines; RMNH = National Natural History Museum Naturalis, Leiden, Netherlands; SMF = Naturmuseum Senckenberg, Frankfurt, Germany; USNM = National Museum of Natural History, Washington, USA; WAM = Western Australian Museum, Perth, Australia; ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMA = Zoological Museum, University of Amsterdam, Netherlands; ZMB = Museum für Naturkunde, Berlin, Germany; ZMUC = Zoological Museum, University of Copenhagen, Denmark.

Update of the checklist of extant monitor lizards by Böhme (2003)

Subgenus *Philippinosaurus* Mertens, 1959

Varanus bitatawa Welton, Siler, Bennett, Diesmos, Duya, Dugay, Rico, van Weerd & Brown, 2010

2010 *Varanus bitatawa* Welton, Siler, Bennett, Diesmos, Duya, Dugay, Rico, van Weerd & Brown, Biol. Lett., 6: 654. – Type locality: Base of the San Ildefonso Peninsula, Sitio Casapsipan, Barangay Casiguran, Municipality of Casiguran, Aurora Province, Luzon Island, Philippines.

2008 *Varanus olivaceus* – Eidenmüller & Philippen (in part), Terralog, 6: 103.

Type specimens: Holotype PNM 9719 (formerly KU 320000), paratypes KU 322188 and PNM 9008.

Distribution: Northern Luzon, Philippines.

Remark: This species was recently separated from *V. olivaceus* based on minor genetic variation, morphological differences and biogeographic evidence (Welton et al. 2010).

Subgenus *Soterosaurus* Ziegler & Böhme, 1997

Varanus s. salvator (Laurenti, 1768)

1768 *Stellio salvator* Laurenti, Synops. Rept.: 56. – Type locality: Sri Lanka.

1758 *Lacerta monitor* part. Linnaeus, Syst. nat., 10 (1): 201. – Type locality: In Indiis (*nomen rejectum* according to ICZN 1959, Opinion 540).

1947 *Varanus salvator kabaragoya* Deraniyagala, Proc. 3rd ann. Sess. Ceylon Assoc. Sci., 2 (Abstr.): 12. – Type locality: Ceylon (= Sri Lanka).

Type specimen: Neotype ZFMK 22092, designated by Koch et al. (2007).

Distribution: Sri Lanka.

Remark: Until recently the nominotypic subspecies had the widest distribution range within the widespread *V. salvator* complex. Due to the revalidation of the subspecies *V. s. macromaculatus* from continental Southeast Asia, the nominotypic subspecies is now restricted to Sri Lanka.

Varanus salvator macromaculatus Deraniyagala, 1944

1944 *Varanus salvator macromaculatus* Deraniyagala, Spol. Zeyl. 24: 60. – Type locality: Siam (= Thailand).

1802 *Tupinambis elegans* Daudin (in part), Hist. nat. Rept., 3: 36. – Type locality: Surinam.

1831 *Tupinambis exilis* Gray in Griffith, Anim. Kingd., 9: 25. – Type locality: India (*nomen dubium*, fide Koch et al. 2007).

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1834 *Varanus vittatus* Lesson in Bélanger, Voyage Ind. Orient. Zool.: 307. – Type locality: Indian subcontinent and islands at the mouth of the Ganges River (*nomen dubium* fide Koch et al. 2007).

1842 *Varanus binotatus* Blyth, J. asiat. Soc. Bengal, 11: 867 (Lapsus fide Mertens 1942).

1942 *Lacertus tupinambis* Mertens (in part, non Lacépède, 1788) Abh. Senckb. Naturf. Ges., 466: 245. – Type locality: unknown (Lapsus fide Brygoo 1987).

1947 *Varanus salvator nicobariensis* Deraniyagala, Proc. 3rd ann. Sess. Ceylon Assoc, Sci., 2, Abstr.: 12. – Type locality: Tillanchong, Nicobar Islands.

1987 *Varanus salvator komaini* Nutphand, J. Thai. Zool. Center, 2 (15): 51. – Type locality: Sea shore areas and small islands in south western Thailand.

2007 *Varanus salvator macromaculatus* – Koch, Auliya, Schmitz, Kuch & Böhme, Mertensiella, 16: 136.

Type specimens: Lectotype MNHN 871, paralectotype MNHN 1884.77, designated by Koch et al. (2007).

Distribution: Thailand, Peninsula Malaysia, Vietnam, southern China, Hainan, Sumatra, and Borneo and smaller off-shore islands.

Remark: This subspecies of *V. salvator* was recently resurrected from the synonymy of the nominotypic subspecies which, due to differences in morphological characters and colour pattern, had to be restricted to Sri Lanka (Koch et al. 2007). At the same time, the melanistic taxon *komaini* from Thailand was identified as a junior synonym of *V. s. macromaculatus* in the absence of morphological differences except for the lack of a light colour pattern. Therefore, the remaining subspecies of *V. salvator* are: *V. s. salvator*, *V. s. macromaculatus*, *V. s. andamanensis*, and *V. s. bivittatus* (Koch et al. 2007).

Varanus cumingi **Martin, 1838**

1838 *Varanus cumingi* Martin, Proc. Zool. Soc. London 1838: 69. – Type locality: Mindanao, Philippines.

1942 *Varanus* (*Varanus*) *salvator cumingi* – Mertens, Abh. Senckb. Naturf. Ges., 466: 256.

2007 *Varanus* (*Soterosaurus*) *cumingi* – Koch, Auliya, Schmitz, Kuch & Böhme, Mertensiella, 16: 168.

Distribution: Islands of the Greater Mindanao region (i.e., Mindanao, Samar, Leyte, and Bohol), Philippines.

Remark: Recently, *V. cumingi* was demonstrated to be specifically distinct from *V. salvator* (Koch et al. 2007). The species was also shown to be polytypic and a new subspecies was described from the northern islands within the species range (Koch et al. 2010).

Varanus c. cumingi **Martin, 1838**

1838 *Varanus cumingi* Martin, Proc. Zool. Soc. London 1838: 69. – Type locality: Mindanao, Philippines.

1991 *Varanus salvator cumingi* – Gaulke (in part), Mertensiella, 2: 154.

Type specimen: Lectotype BMNH 1946.8.31.5, designated by Koch et al. (2007).

Distribution: Restricted to Mindanao and off-shore islands, Philippines.

Varanus cumingi samarensis **Koch, Gaulke & Böhme, 2010** (Fig. 1D)

2010 *Varanus cumingi samarensis* Koch, Gaulke & Böhme, Zootaxa, 2440: 19 – Type locality: San Augustin near Gandara, Samar Island, Philippines.

1991 *Varanus salvator cumingi* – Gaulke (in part), Mertensiella, 2: 161.

Type specimens: Holotype ZFMK 64713, paratype ZFMK 64712.

Distribution: Samar, Bohol, and Leyte, Philippines.

Varanus marmoratus **(Wiegmann, 1834)**

1834 *Hydrosaurus marmoratus* Wiegmann, in Meyen, Reise um die Erde, 3: 446. – Type locality: San Mat(h)eo village or Talim Island, Laguna Bay, near Manila, Luzon, Philippines.

1829 *M*[*onitor*] *marmoratus* Cuvier, Règne animal 2(2): 26. (*nomen nudum* fide Mertens 1942; Good et al. 1993).

1844 *Monitor bivittatus philippensis* Schlegel, Abb. Amphib.: x. – Type locality: Manila, Luzon.

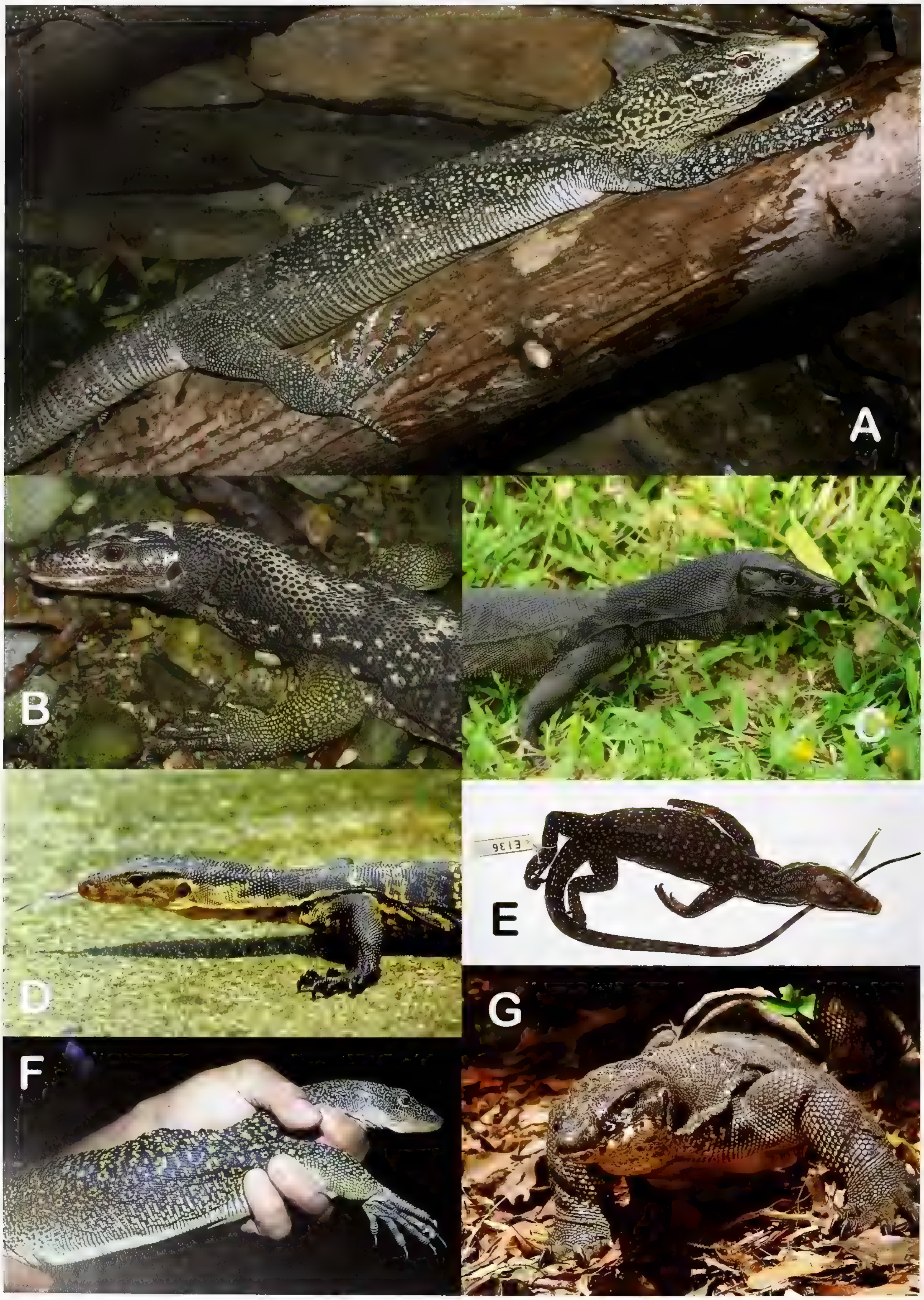

Fig. 1. Fig. 1: Some monitor lizards described after Böhme's (2003) checklist and species where the taxonomic status has changed since. A: *Varanus boehmei* Jacobs, 2003 (photo T. Ziegler); B: *V. nuchalis*, revalidated species status (photo M. Gaulke); C: *V. togianus*, revalidated species status (photo A. Koch); D: *V. cumingi samarensis* Koch, Gaulke & Böhme, 2010 (photo M. Gaulke); E: *V. rasmusseni* Koch, Gaulke & Böhme, 2010, juvenile paratype ZFMK 89391 (photo A. Koch); F: *V. lirungensis* Koch, Arida, Schmitz, Böhme & Ziegler, 2009 (photo M. Auliya); G: *V. palawanensis* Koch, Gaulke & Böhme, 2010 (photo I. Langlotz).

1876 *Varanus manilensis* von Martens, Preuß. Exped. Ostas. Zool., 1: 196. (Lapsus fide Mertens 1942).

1942 *Varanus* (*Varanus*) *salvator marmoratus* – Mertens, Abh. Senckb. Naturf. Ges., 466: 254.

1944 *Varanus salvator philippinensis* Deraniyagala, Spol. Zeylan., 24: 61. – Type locality: Luzon.

1997 *Varanus* (*Soterosaurus*) *salvator marmoratus* – Ziegler & Böhme, Mertensiella, 8: 177.

2007 *Varanus* (*Soterosaurus*) *marmoratus* – Koch, Auliya, Schmitz, Kuch & Böhme, Mertensiella, 16: 161.

Type specimen: Lectotype ZMB 470, designated by Mertens (1942).

Distribution: Restricted to Luzon and some off-shore islands, Philippines.

Remark: Originally, Wiegmann (1834) based his description on two voucher specimens (Koch et al. 2007). The second larger syntype, however, which should have paralectotype status, is missing (Good et al. 1993). Recently, *V. marmoratus* was shown to represent a collective species (Koch et al. 2010). The disjunct island populations of the Greater Palawan region and the Sulu Archipelago were allocated to two new species (see below).

Varanus nuchalis (Günther, 1872) (Fig. 1B)

1872 *Hydrosaurus nuchalis* Günther, Proc. Zool. Soc. London, 1872: 145. – Type locality: Philippines.

1942 *Varanus* (*Varanus*) *salvator nuchalis* – Mertens, Abh. Senckb. Naturf. Ges., 466: 258.

1997 *Varanus* (*Soterosaurus*) *salvator nuchalis* – Ziegler & Böhme, Mertensiella, 8: 177.

2007 *Varanus* (*Soterosaurus*) *nuchalis* – Koch, Auliya, Schmitz, Kuch & Böhme, Mertensiella, 16: 165.

Type specimen: Holotype BMNH 1946.9.1.17.

Distribution: Islands of Negros, Panay, Masbate, Ticao, and Cebu, Philippines.

Remark: Despite a high variation in colour pattern, a recent study could not document a correlation between colour pattern and distribution (Koch et al. 2010).

Varanus palawanensis Koch, Gaulke & Böhme, 2010 (Fig. 1G)

2010 *Varanus palawanensis* Koch, Gaulke & Böhme, Zootaxa, 2446: 33. – Type locality: Tabon, Palawan Island, Philippines.

1942 *Varanus* (*Varanus*) *salvator marmoratus* – Mertens (in part), Abh. Senckb. Naturf. Ges., 466: 254.

1991 *Varanus salvator marmoratus* – Gaulke (in part), Mertensiella, 2: 154.

2007 *Varanus* (*Soterosaurus*) *marmoratus* – Koch, Auliya, Schmitz, Kuch & Böhme (in part), Mertensiella, 16: 161.

Type specimens: Holotype SMF 73912, paratypes SMF 73914–15, BMNH 94.6.30.19, BMNH 94.6.30.20, MNHN 1884-187, ZMUC E78, and ZFMK 89691 (formerly SMF 73913).

Distribution: Islands of Greater Palawan (Palawan, Balabac and the Calamian Island group) and Sibutu Island within the Sulu Archipelago, Philippines.

Remark: Traditionally, the populations of Palawan and adjacent islands were allocated to *V. marmoratus*, but recent investigations confirmed their morphological distinctness (Koch et al. 2010).

Varanus rasmusseni Koch, Gaulke & Böhme, 2010 (Fig. 1E)

2010 *Varanus rasmusseni* Koch, Gaulke & Böhme, Zootaxa, 2446: 28. – Type locality: Tarawakan, north of Batu-Batu, Tawi-Tawi Island, Sulu Archipelago, Philippines.

1992 *Varanus salvator marmoratus* – Gaulke (in part), Hamadryad, 17: 21.

2007 *Varanus* (*Soterosaurus*) cf. *marmoratus* – Koch, Auliya, Schmitz, Kuch & Böhme, Mertensiella, 16: 163.

Type specimens: Holotype ZMUC R42151, paratype ZFMK 89391 (formerly ZMUC R42153).

Distribution: Only known from the type locality, but probably also on other islands of the Tawi-Tawi island group, Philippines.

Remark: Recent morphological investigations demonstrated the specific distinctness of the Tawi-Tawi population which was formerly assigned to *V. marmoratus* (Koch et al. 2010).

Varanus togianus (Peters, 1872) (Fig. 1C)

1872 *Monitor* (*Hydrosaurus*) *togianus* Peters, Monatb. Kön. Preuss. Akad. Wiss., 1872: 582. – Type locality: Timotto, Togian (= Togean) Islands, Central Sulawesi, Indonesia.

1942 *Varanus* (*Varanus*) *salvator togianus* – Mertens, Abh. Senckb. Naturf. Ges., 466: 253.

1997 *Varanus* (*Soterosaurus*) *salvator togianus* – Ziegler & Böhme, Mertensiella, 8: 177.

2007 *Varanus* (*Soterosaurus*) *togianus* – Koch, Auliya, Schmitz, Kuch & Böhme, Mertensiella, 16: 156.

Type specimens: Lectotype ZMB 7388, paralectotype ZMB 7389, by designation of Mertens (1942).

Distribution: Sulawesi, except the northern peninsula.

Remark: Recent investigations revealed this endemic Sulawesi taxon to be specifically distinct from *V. salvator* (Koch et al. 2007) and polytypic (Koch et al. unpubl. data).

Subgenus *Euprepiosaurus* Fitzinger, 1843

Varanus indicus species group

Varanus lirungensis Koch, Arida, Schmitz, Böhme & Ziegler, 2009 (Fig. 1F)

2009 *Varanus lirungensis* Koch, Arida, Schmitz, Böhme & Ziegler, Austr. J. Zool., 57: 33. – Type locality: near Lirung, Salibabu Island, Talaud Islands, Indonesia.

1915 *Varanus indicus* – de Rooij (in part), Rept. Indo-Austr. Arch., 1: 149.

1942 *Varanus* (*Varanus*) *indicus indicus* – Mertens (in part), Abh. Senckb. Naturf. Ges., 466: 263.

Type specimens: Holotype MZB Lac. 5178, paratypes MZB Lac. 5176-77, 5179-80, ZFMK 87587 (formerly ZMA 15411a), ZMA 15411b.

Distribution: Only known from the type locality.

Remark: *V. lirungensis* represents the most north-western member of the *V. indicus* species group (Koch et al. 2009).

Varanus obor Weijola & Sweet, 2010

2010 *Varanus obor* Weijola & Sweet, Zootaxa, 2434: 18. – Type locality: Soela-Bési (= Sanana Island), Sula Islands, Moluccas, Indonesia.

Type specimen: Holotype RMNH 7225.

Distribution: Only known from the type locality.

Remark: *V. obor* represents the latest discovery of a member of the *V. indicus* species group. Nothing is known about its conservation status (Weijola & Sweet 2010).

Varanus rainerguentheri Ziegler, Böhme & Schmitz, 2007

2007 *Varanus rainerguentheri* Ziegler, Böhme & Schmitz, Mitt. Mus. Nat.kd. Berlin, Suppl. 83: 110. – Type locality: Jailolo, Halmahera Island, Moluccas, Indonesia.

2005 *Varanus* cf. *indicus* – Böhme & Ziegler, Salamandra, 41: 57.

Type specimens: Holotype ZFMK 85404, paratype USNM 237438.

Distribution: Northern Moluccan islands of Halmahera, Ternate, Tidore, Morotai, Bacan, Gebe and Obi.

Remark: Originally, *V. rainerguentheri* was only known from its type locality (Ziegler et al. 2007a), but recent field studies showed that this species occurs over a wider range in the Moluccas (Weijola 2010).

Varanus zugorum Böhme & Ziegler, 2005

2005 *Varanus zugorum* Böhme & Ziegler, Salamandra, 41(1/2): 52. – Type locality: Kampung Pasir Putih, Jailolo district, Halmahera Island, Moluccas, Indonesia.

Type specimen: Holotype USNM 237439.

Distribution: Only known from the type locality.

Remark: *V. zugorum* appears to be the rarest or at least known monitor lizard of all species described, known only from the holotype specimen. Recent field work on Halmahera Island failed to record this secretive species (Setiadi & Hamidy 2006; Weijola 2010; Awal Riyanto, Bogor, pers. comm. viii.2010). Only one putative photograph of a live specimen exists (see Böhme & Ziegler 2005).

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Varanus prasinus species group

Varanus beccarii (Doria, 1874)

1874 *Monitor Beccarii* Doria, Ann. Mus. Civ. Stor. Nat. Genova, 6: 331. – Type locality: Wokam, Aru Islands, Indonesia.

1942 *Varanus* (*Odatria*) *prasinus beccarii* – Mertens, Abh. Senckb. Naturf. Ges., 466: 296.

2003 *Varanus* (*Euprepiosaurus*) *prasinus beccarii* – Böhme, Zool. Verh., 341: 25.

2007 *Varanus* (*Euprepiosaurus*) *beccarii* – Ziegler, Schmitz, Koch & Böhme, Zootaxa, 1472: 15.

Type specimens: Syntypes ZMB 7993, MSNG 28723.

Distribution: Restricted to the Aru Islands.

Remark: In the past, the taxon *beccarii* was considered a subspecies of *V. prasinus* (e.g. Mertens 1942; Ziegler & Böhme 1997). Recently, Ziegler et al. (2007b) demonstrated that *V. beccarii* is distinct from the latter species. The species is potentially threatened by the international trade in live specimens.

Varanus boehmei Jacobs, 2003 (Fig. 1A)

2003 *Varanus boehmei* Jacobs, Salamandra, 39(2): 66. – Type locality: Waigeo Island, West Papua, Indonesia.

Type specimens: Holotype ZFMK 77837, paratypes ZFMK 82826, ZFMK 84000, ZMA 21702 (formerly ZFMK 79122) and three further specimens which were still alive and will be deposited in ZFMK after their demise.

Distribution: Only known from the type locality.

Remark: Due to its restricted distribution range and its exploitation for the international pet trade, *V. boehmei* must be considered threatened.

Varanus reisingeri Eidenmüller & Wicker, 2005

2005 *Varanus reisingeri* Eidenmüller & Wicker, Sauria, 27(1): 4. – Type locality: Insel Misol (= Misool Island) off the west coast of West Papua, New Guinea, Indonesia.

1942 *Varanus* (*Odatria*) *prasinus prasinus* – Mertens (in part), Abh. Senckb. Naturf. Ges., 466: 292.

Type specimens: Holotype SMF 83679, the two paratypes are still alive and will be deposited in SMF after their demise (Bernd Eidenmüller, Frankfurt, pers. comm. xii.2010).

Distribution: Only known from the type locality.

Remark: The taxonomic validity of this species remains uncertain because diagnostic morphological characters largely overlap with *V. prasinus* from New Guinea. As the former species, *V. reisingeri* is also potentially threatened by exploitation for the pet trade.

Subgenus *Odatria* Gray, 1838

Varanus bushi Aplin, Fitch & King, 2006

2006 *Varanus bushi* Aplin, Fitch & King, Zootaxa, 1313: 24. – Type locality: Marandoo, Western Australia (22° 37'S 118° 08' E).

1980 *Varanus caudolineatus* – Storr (in part), Rec. West. Austr. Mus., 8: 250.

Type specimens: Holotype WAM R108999, paratypes WAM R54230, WAM R56834, and WAM R62171.

Distribution: Endemic to the Pilbara region of Western Australia.

Remark: *V. bushi* was described as morphologically and genetically distinct from its closest relatives *V. caudolineatus* and *V. gilleni*. All three Australian dwarf monitor lizards display complex patterns of sexual dimorphism (Aplin et al. 2006).

Subgenus: Incertae sedis

Varanus spinulosus Mertens, 1941

1941 *Varanus indicus spinulosus* Mertens, Senckenbergiana, 23: 269. – Type locality: Georgs-Insel (= St. George Island or San Jorge Island), near Santa Isabel (= Ysabel) Island, Solomon Islands.

1942 *Varanus* (*Varanus*) *indicus spinulosus* – Mertens, Abh. Senckb. Naturf. Ges., 466: 271.

1994 *Varanus spinulosus* – Sprackland, Herpetofauna, 24 (2): 34.

1997 *Varanus* (*Euprepiosaurus*) *spinulosus* – Ziegler & Böhme, Mertensiella, 8: 14.

2007 *Varanus* (subgen. inc. sed.) *spinulosus* – Böhme & Ziegler, Mertensiella, 16: 105.

Type specimen: Holotype NMW 23387 (formerly NMW 3709).

Distribution: San Jorge and Santa Isabel Islands, Solomon Islands, and Bougainville Island, Papua New Guinea.

Remark: For almost 50 years, this rare monitor lizard species was only known from the holotype (Sprackland 1993). The former collection number of the type was originally assigned by Mertens (1941, 1942) and still applied by de Lisle (2009). Tiedemann et al. (1994) and Böhme & Koch (2010) provided the current number. Sprackland (1994) elevated *spinulosus* to full species status. Recently, the distribution range of *V. spinulosus* was extended, when the species was newly recorded from Bougainville Island and its occurrence was confirmed on the island of Santa Isabel (Böhme & Ziegler 2007; Dwyer 2008).

V. spinulosus was formerly allocated to the *V. indicus* species group of the subgenus *Euprepiosaurus* (see Ziegler & Böhme 1997), but a new monotypic subgenus is discussed based on new genital morphological findings (Böhme & Ziegler 2007).

DISCUSSION

In total, ten new species and one new subspecies were introduced to science since Böhme's (2003) checklist. Nine of the species (i.e., 90%) and the subspecies were described from islands of the Indo-Australian Archipelago. Only one new species, *V. bushi*, was recently identified from Western Australia (Aplin et al. 2006). In addition, five taxa (*beccarii*, *cumingi*, *marmoratus*, *nuchalis*, and *togianus*) were re-elevated to full species status due to morphological (e.g., scale counts, morphometrics, colour pattern) and/or genetical idiosyncrasies, thus bringing the global diversity to 73 (including 21 subspecies). This represents an increase in species diversity of 20% since 2003. Particularly 2010 has been a very productive year for the increase of monitor lizard diversity. Four new species and one new subspecies were described from Indonesia and the Philippines within the first half of 2010 (Koch et al. 2010; Weijola & Sweet 2010; Welton et al. 2010).

Descriptions of new monitor lizard species since 2003 mainly refer to two different taxonomic groups, the Southeast Asian and Indo-Australian subgenera *Soterosaurus* and *Euprepiosaurus*, with two and six new species, respectively. In addition, the taxonomic status of several members of the subgenus *Soterosaurus* has changed. While this subgenus was hitherto considered monotypic with *V. salvator* being the only, albeit polytypic species with eight recognized subspecies (Böhme 2003), the Philippine subspecies *cumingi*, *marmoratus*, and *nuchalis*, and *togianus* from Sulawesi were re-elevated to their original species status (Koch et al. 2007), thus resulting in a species complex of closely related allies. Additionally, one subspecies (*V. salvator macromaculatus*) of the Southeast Asian water monitor lizard was revalidated, whereas the younger melanistic taxon *komaini* was synonymized with the former (Koch et al. 2007).

With currently 22 recognized species, the subgenus *Euprepiosaurus* has displaced the Australian *Odatria* as the most species-rich subgenus of varanids. Within *Euprepiosaurus*, the new species descriptions are unevenly distributed over the two species groups involved, viz. the Pacific monitors around *V. indicus* and the tree monitors around *V. prasinus*, respectively. The latter group experienced only two new species descriptions (i.e., *V. boehmei* and *V. reisingeri*) and currently comprises nine allopatric species from New Guinea and its offshore islands. On the other hand, four new species were added to the *V. indicus* species group leading to a total of 13 recognized species, at least four of which occur in sympatry on New Guinea and Halmahera in the northern Moluccas. Among these recently described Pacific monitor lizard species, next to morphologically cryptic taxa, such as *V. lirungensis* or *V. rainerguentheri*, there are also strikingly different species with idiosyncratic features in morphology and colour pattern, such as the melanistic *V. obor* and the silver-coloured *V. zugorum*. Five years after its formal description and despite repeated field trips to the northern Moluccas (Setiadi & Hamidy 2006; Weijola 2010; Awal Riyanto, Bogor, pers. comm. viii.2010), the latter species is still only known from the holotype specimen and has thus to be regarded the rarest and at least known varanid species.

Böhme (2003) already recognized a taxonomic trend towards a reduction of polytypic monitor lizard species by the elevation of nominal subspecies to species rank. Certainly, this trend still continues as seen in the *V. salvator* complex (Koch et al. 2007). The description of a new subspecies of *V. cumingi* from the Philippines (Koch et al. 2010), however, demonstrates that a distinction is still made between the degree of morphological (e.g., morphometrics and scalation features) and molecular differentiation (i.e. characteristics of the full species category) and mere geographically correlated differences in colour pattern (i.e. diagnostic features of subspecies).

CONCLUSIONS

Because taxonomy is a dynamic discipline, further changes and additions to the list of extant monitor lizards are to be expected in the future. This will include new species descriptions – either real discoveries or by the splitting of already recognized species – as well as a change of the taxonomic status. Therefore, we are aware that this updated checklist can only represent the latest state of art and may already be outdated by the time of publication. In terms of conservation purposes, it is essential to refer to these most recent checklists, and with the increase of monitor lizard diversity especially in the Indo-Australian realm, there is definitely a need to establish user-friendly identification tools for a vertebrate group globally sought after within the international pet and reptile leather trade.

We do wish that our contribution will serve as a useful supplement to the checklist of the living monitor lizards of the world by Böhme (2003) for all those who are interested in or concerned with the diversity of monitor lizards.

Acknowledgments. The fact, that Wolfgang Böhme was involved in most of the recent taxonomic changes and additions to the global checklist of varanids together with the naming of one new species, viz. *V. boehmei*, after him, reflect his internationally renowned competence and eminent position in systematic monitor lizard research. On the occasion of his retirement, we hereby wish to dedicate this contribution to Professor Dr. Wolfgang Böhme, Vice Director, Head of the Vertebrate Department and Curator of Herpetology for 39 years at the Zoologisches Forschungsmuseum Alexander Koenig in Bonn, Germany. We are deeply indebted to Wolfgang Böhme, who initiated and supervised our careers related to varanid research.

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New discoveries of amphibians and reptiles from Vietnam

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Abstract. We provide a list of 21 new amphibian and reptilian species and subspecies discoveries from Vietnam, including one new snake genus, published after the comprehensive overview by Nguyen et al. (2009). The new herpetofauna representatives are introduced inclusive of the original description, type locality, English and Vietnamese names, as well as current distribution.

Key words. Vietnam, herpetofauna, new species.

INTRODUCTION

Although Vietnam has one of the world's richest amphibian and reptilian fauna, as revealed particularly through surveys by Vietnamese scientists and their international collaborators during the past quarter century, the study of its herpetofauna was long overshadowed by research in India, China, and the East Indies (Adler 2009). The first significant summary of the Vietnamese herpetofauna was written by Morice (1875), in which 13 amphibians and 114 species of reptiles including the marine species were listed. Ten years later, Tirant (1885) published a 104-pages book containing 166 species of herpetofauna from Vietnam and Cambodia. Subsequently, the following staff members or associates of the Muséum d'Histoire Naturelle, Paris, published specific studies of Vietnamese amphibians and reptiles: Léon Vaillant (1834–1914), François Mocquard (1834–1917), Jacques Pellegrin (1873–1944), Paul Chabanaud (1876–1959), Fernand Angel (1881–1950), and René Bourret (1884–1957), who was the only one of the afore mentioned zoologists who ever set foot in Vietnam (Adler 2009).

It was René Bourret, originally a geologist, who became the leading authority on Vietnamese herpetofauna. From 1927 until 1947 he published a series of papers and books of Indochinese and specifically on Vietnamese herpetology. Besides the publication of several identification manuals, he is most famous for a substantial series of monographs of Indochinese herpetology, which are to date the most important background on the subject (Bourret 1936a, b, 1941, 1942). In total, René Bourret reported of 177 lizard taxa (i.e., species and subspecies), 245 snake taxa, 45 turtle taxa and 171 amphibian taxa for the Indochinese region (Nguyen 2006).

Because of the French Indochina War, no remarkable herpetological studies were undertaken in the period from 1946 to 1954. In 1954, when northern Vietnam attained independence from France, Vietnamese herpetologists began to conduct herpetological field surveys predominantly in northern Vietnam, and the first lists and keys to the species of Vietnamese amphibians and reptiles were compiled by Dao (e.g., 1977, 1978, 1979, 1981, 1982), including 363 species in total, but with inaccuracies. Another noteworthy key to snakes of southern Vietnam was written during the Second Indochina War, better known in the West as Vietnam War, by Campden-Main (1970), who had served several years as a medic with American forces stationed in Vietnam.

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The end of the Vietnam War in 1975 marked the beginning of another period of biodiversity research in Vietnam (Sterling et al. 2006). Thereafter, an increasing engagement in herpetological field work mainly by Russian institutions was observable, which is still persistent. Eventually, in the last 30 years many international herpetological cooperations emerged, which led to an enormous increase in new records and species descriptions from Vietnam (see overview in Nguyen 2006). As a consequence, the updated checklist by Nguyen et al. (2005) comprised 458 species, viz., 162 species of amphibians and 296 species of reptiles, which included more than 100 additional species compared with the previous checklist of the herpetofauna of Vietnam by Nguyen & Ho (1996). Furthermore, the most actual list (Nguyen et al. 2009) covers 12 additional species of amphibians and 64 additional species of reptiles compared with Nguyen et al. (2005).

On the occasion of this Proceedings Volume addicted to Professor Dr. Wolfgang Böhme, Vice Director, Head of the Vertebrate Department and Curator of Herpetology at the Zoological Research Museum Alexander Koenig, Bonn, Germany, we provide a list of new amphibian and reptilian discoveries from Vietnam that were published subsequent to the comprehensive overview provided by Nguyen et al. (2009). We would like to dedicate this paper to Wolfgang Böhme, who supervised the PhD theses of both authors (T. Ziegler: 1997–2000; T.Q. Nguyen 2007–2011) and thus decisively brought forward herpetodiversity research in Vietnam.

MATERIAL AND METHODS

We herein compiled species' descriptions that were formally published after the appearance of Nguyen et al. (2009). We therefore followed the style and taxonomic arrangement provided by the latter authors.

Abbreviations are as follows: AMNH = American Museum of Natural History, New York, USA; AMS = Australian Museum, Sydney, Australia; IEBR = Institute of Ecology and Biological Resources, Hanoi, Vietnam; ITBCZ = Institute of Tropical Biology, Collection of Zoology, Ho Chi Minh City, Vietnam; LSUHC = La Sierra University, Herpetological Collection, La Sierra University, Riverside, California, USA; UNS = Zoological Collection of the University of Natural Sciences, Ho Chi Minh City, Vietnam; VNMN = Vietnam National Museum of Nature, Hanoi, Vietnam; ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZISP = Zoological Institute, St. Petersburg, Russia; a.s.l. = above sea level.

LIST OF NEW SPECIES AND SUBSPECIES SINCE NGUYEN ET AL. (2009)

Amphibia

Anura

Megophryidae

Leptolalax applebyi Rowley & Cao, 2009

Leptolalax applebyi J.J.L. Rowley & T.T. Cao, 2009, Zootaxa 2198: 52.

Holotype: AMS R171703.

Type locality: Song Thanh Proposed Nature Reserve, Phouc Son (Phuoc Son) District, Quang Nam Province, Vietnam, 1,402 m a.s.l.

English name: Appleby's Asian Toad.

Vietnamese name: Coc may ap-li-bai.

Distribution: This species is currently known only from the type locality.

Ranidae

Odorrana geminata Bain, Stuart, Nguyen, Che & Rao, 2009

Odorrana geminata R.H. Bain, B.L. Stuart, T.Q. Nguyen, J. Che & D.-Q. Rao, 2009, Copeia 2: 355.

Holotype: AMNH 163782.

Type locality: Mount Tay Con Linh II, Cao Bo Commune, Vi Xuyen District, Ha Giang Province, Vietnam, 1,420 m a.s.l.

English name: Geminated Cascade Frog.

Vietnamese name: Ech bam da hoa.

Distribution: This species (Fig. 1a) is currently known only from montane areas in northeastern Vietnam (Ha Giang and Cao Bang provinces) and southeastern Yunnan Province, China.

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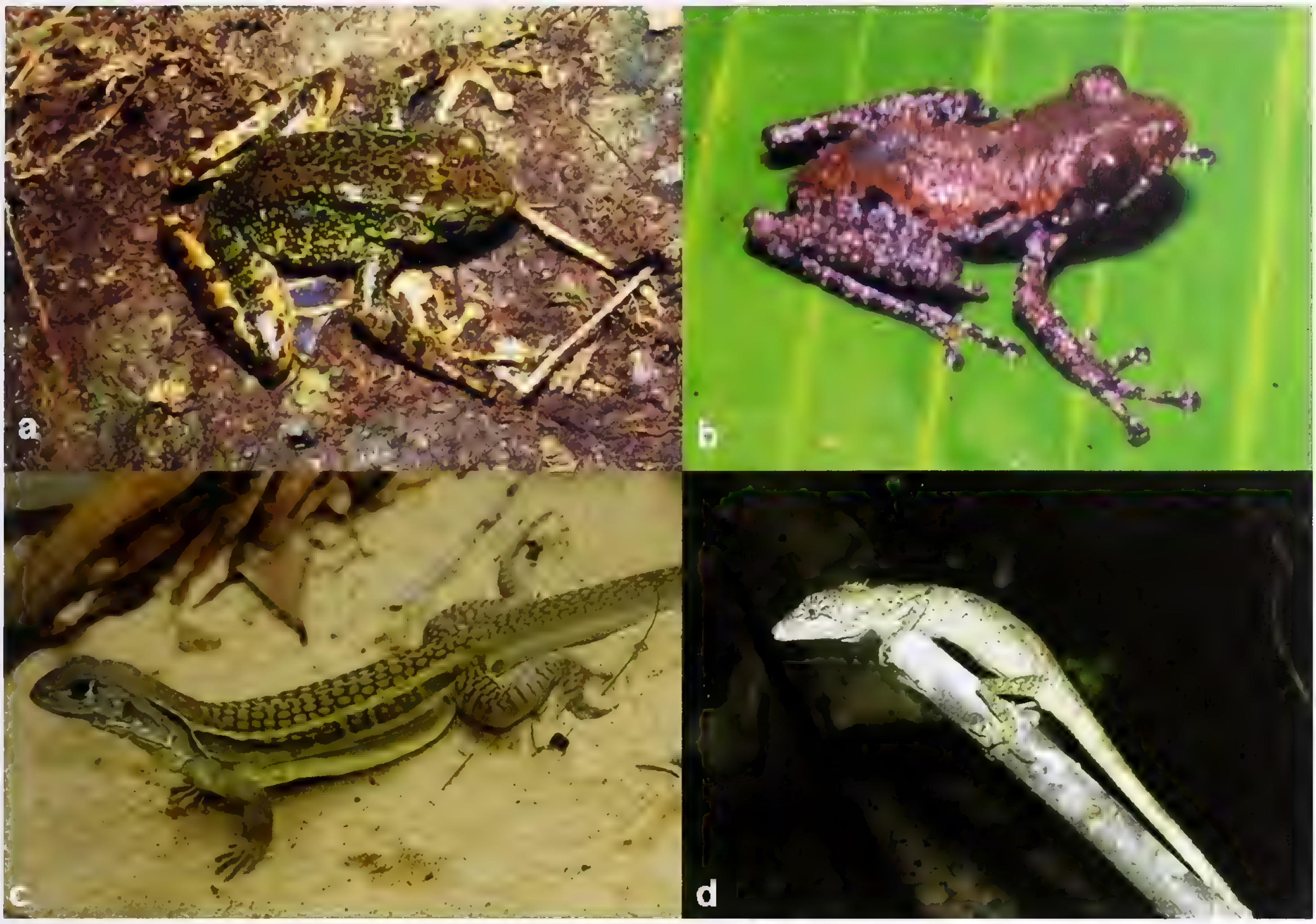

Fig. 1. a) *Odorrana geminata* from Ha Giang Province, Photo T.Q. Nguyen; b) *Theloderma lateriticum* from Lao Cai Province, Photo T.Q. Nguyen; c) *Leiolepis ngovantrii* from Ba Ria–Vung Tau Province, Photo L.L. Grismer; and d) *Pseudocalotes ziegleri* from Kon Tum Province, Photo C.T. Ho.

Rhacophoridae

Theloderma lateriticum Bain, Nguyen & Doan, 2009

Theloderma lateriticum R.H. Bain, T.Q. Nguyen & K.V. Doan, 2009, Zootaxa 2191: 60.

Holotype: AMNH 168757/IEBR A. 0860.

Type locality: Nam Tha Commune, Van Ban District, Lao Cai Province, Vietnam, 1,300–1,400 m a.s.l.

English name: Brick-red Bug-eyed Frog.

Vietnamese name: Ech cay san do.

Distribution: This species (Fig. 1b) is currently known only from the type locality.

Reptilia

Squamata

Sauria

Agamidae

Leiolepis ngovantrii Grismer & Grismer, 2010

Leiolepis ngovantrii J.L. Grismer & L.L. Grismer, 2010, Zootaxa 2433: 52.

Holotype: LSUHC 9234.

Type locality: Binh Chau–Phuoc Buu Nature Reserve, Xuyen Moc District, Ba Ria–Vung Tau Province, Vietnam, 30 m a.s.l.

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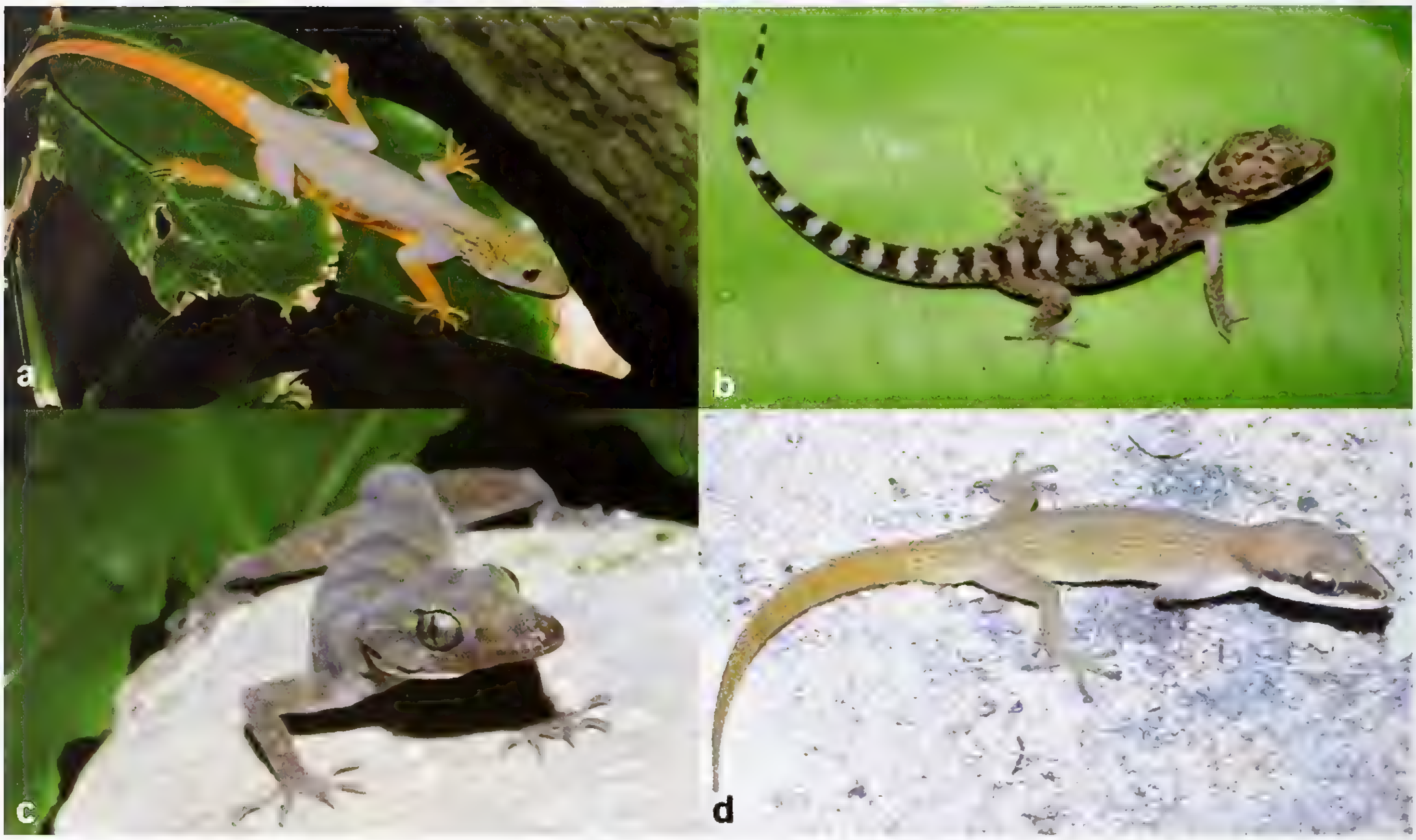

Fig. 2. a) *Cnemaspis psychedelica* from Ca Mau Province, Photo L.L. Grismer; b) *Cyrtodactylus cattienensis* from Dong Nai Province, Photo P. Geissler; c) *Cyrtodactylus roesleri* from Quang Binh Province, Photo T. Ziegler; and d) *Dixonius aaronbaueri* from Ninh Thuan Province, Photo T.V. Ngo.

English name: Ngovantri's Butterfly Lizard.

Vietnamese name: Nhong cat ngo van tri.

Distribution: This species (Fig. 1c) is currently known only from Vietnam (Ba Ria–Vung Tau Province).

Pseudocalotes ziegleri Hallermann, Nguyen, Orlov & Ananjeva, 2010

Pseudocalotes ziegleri J. Hallermann, T.Q. Nguyen, N. Orlov & N. Ananjeva, 2010, Russ. J. Herpetol. 17(1): 32.

Holotype: IEBR 330.

Type locality: Nuoc Ka forest, near Mang Canh, Kon Plong District, Kon Tum Province, Vietnam, ca. 1,200 m a.s.l.

English name: Ziegler's Tree Lizard.

Vietnamese name: Nhong zig-lo.

Distribution: This species (Fig. 1d) is currently known only from Vietnam (Kon Tum Province).

Remarks: Specimens identified as *Pseudocalotes floweri* from Kon Tum Province (Bain et al. 2007) were subsequently re-identified as *P. ziegleri* by Hallermann et al. (2010).

Gekkonidae

Cnemaspis psychedelica Grismer, Ngo & Grismer, 2010

Cnemaspis psychedelica L.L. Grismer, T.V. Ngo & J.L. Grismer, 2010, Zootaxa 2352: 48.

Holotype: UNS 0444.

Type locality: Hon Khoai Island, Ngoc Hien District, Ca Mau Province, Vietnam.

English name: Psychedelic Gecko.

Vietnamese name: Tac ke duoi vang.

Distribution: This species (Fig. 2a) is currently known only from the type locality.

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***Cyrtodactylus cattienensis* Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen & Ziegler, 2009**

Cyrtodactylus cattienensis P. Geissler, R. Nazarov, N.L. Orlov, W. Böhme, T.M. Phung, T.Q. Nguyen & T. Ziegler, 2009, Zootaxa 2161, 21.

Holotype: IEBR A.0856.

Type locality: Cat Tien National Park, Dong Nai Province, Vietnam, 120 m a.s.l.

English name: Cattien Bent-toed Gecko.

Vietnamese name: Thach sung ngon cat tien.

Distribution: This species (Fig. 2b) is currently known only from Vietnam (Ba Ria-Vung Tau and Dong Nai provinces).

***Cyrtodactylus roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz, 2010**

Cyrtodactylus roesleri T. Ziegler, R. Nazarov, N. Orlov, T.Q. Nguyen, T.N. Vu, K.N. Dang, T.H. Dinh & A. Schmitz, 2010, Zootaxa, 2413: 24.

Holotype: ZFMK 89377.

Type locality: Phong Nha–Ke Bang National Park, Minh Hoa District, Quang Binh Province, Vietnam.

English name: Roesler's Bent-toed Gecko.

Vietnamese name: Thach sung ngon ro-x-lo.

Distribution: This species (Fig. 2c) is currently known only from the type locality.

***Cyrtodactylus yangbayensis* Ngo & Chan, 2010**

Cyrtodactylus yangbayensis T.V. Ngo & K.O. Chan, Zootaxa, 2504: 48.

Holotype: UNS 0476.

Type locality: Yang Bay Waterfall, Dien Khanh District, Khanh Hoa Province, southern Vietnam, 500–600 m a.s.l.

English name: Yangbay Bent-toed Gecko.

Vietnamese name: Than lan chan ngon yang bay.

Distribution: This species is currently known only from the type locality in Khanh Hoa Province.

***Dixonius aaronbaueri* Ngo & Ziegler, 2009**

Dixonius aaronbaueri T.V. Ngo & T. Ziegler, 2009, Zoosyst. Evol., 85(1): 119.

Holotype: UNS 0284.

Type locality: Binh Tien Forest Station, Ninh Hai District, Nui Chua National Park, Ninh Thuan Province, southern Vietnam, 4–5 m a.s.l.

English name: Aaron Bauer's Leaf-toed Gecko.

Vietnamese name: Than lan chan la a-ron-bau-o.

Distribution: This species (Fig. 2d) is currently known only from the type locality.

***Gekko canhi* Rösler, Nguyen, Doan, Ho, Nguyen & Ziegler, 2010**

Gekko canhi H. Rösler, T.Q. Nguyen, K.V. Doan, C.T. Ho, T.T. Nguyen & T. Ziegler, 2009, Zootaxa 2329: 57.

Holotype: IEBR A.0910.

Type locality: Huu Lien, Huu Lung, Lang Son Province, North Vietnam.

English name: Canh's Gecko.

Vietnamese name: Tac ke canh.

Distribution: This species (Fig. 3a) is currently known only from northern Vietnam (Lang Son and Lao Cai provinces).

***Gekko russelltraini* Ngo, Bauer, Wood & Grismer, 2009**

Gekko russelltraini T.V. Ngo, A.M. Bauer, P.L. Jr. Wood & J.L. Grismer, 2009, Zootaxa 2238: 34.

Holotype: UNS 0293.

Type locality: Chua Chan Mountain, Suoi Cat Commune, Xuan Loc District, Dong Nai Province, Vietnam, ca. 100 m a.s.l.

English name: Russell Train's Marble Gecko.

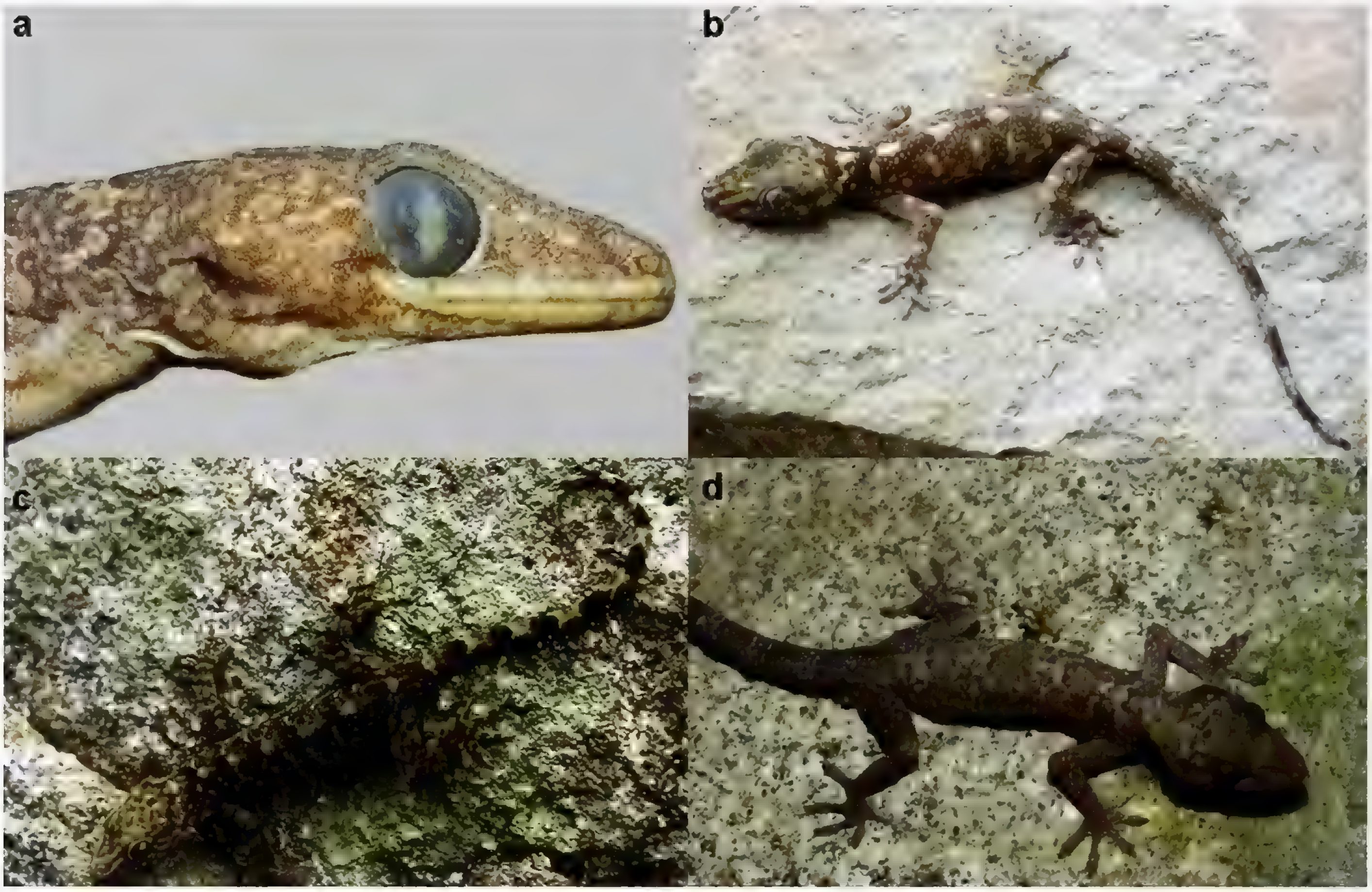

Fig. 3. a) Portrait of preserved *Gekko canhi* from Lang Son Province, Photo T. Ziegler; b) *Gekko russelltraini* from Dong Nai Province, Photo T.V. Ngo; c) *Gekko takouensis* from Binh Thuan Province, Photo S.N. Nguyen; and d) *Gekko vietnamensis* from An Giang Province, Photo S.N. Nguyen.

Vietnamese name: Than lan da ru-xen-tren.

Distribution: This species (Fig. 3b) is currently known only from Vietnam (Dong Nai Province).

Gekko takouensis **Ngo & Gamble, 2010**

Gekko takouensis T.V. Ngo & T. Gamble, 2010, Zootaxa 2346: 18.

Holotype: UNS 0491.

Type locality: Ta Kou Mountain, Ham Thuan Nam District, Binh Thuan Province, Vietnam, 425 m a.s.l.

English name: Takou Marbled Gecko.

Vietnamese name: Than lan da ta kou.

Distribution: This species (Fig. 3c) is currently known only from the type locality.

Gekko vietnamensis **Nguyen, 2010**

Gekko vietnamensis S.N. Nguyen, 2010, Zootaxa 2501: 55.

Holotype: ITBCZ 667.

Type locality: Tuc Dup Hill, An Giang Province, southern Vietnam, 43 m a.s.l.

English name: Vietnam Gecko

Vietnamese name: Tac ke viet nam.

Distribution: This species (Fig. 3d) is currently known only from the type locality.

Scincidae

Scincella apraefrontalis **Nguyen, Nguyen, Böhme & Ziegler 2010**

Scincella apraefrontalis T.Q. Nguyen, S.V. Nguyen, W. Böhme & T. Ziegler, 2010, Folia. Zool., 59(2): 116.

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Holotype: IEBR A.0832.

Type locality: Huu Lien Nature Reserve, Huu Lung District, Lang Son Province, Vietnam, ca. 200 m a.s.l.

English name: Huulien Ground Skink.

Vietnamese name: Than lan co huu lien.

Distribution: This species is only known from Lang Son Province, northeastern Vietnam.

***Tropidophorus boehmei* Nguyen, Nguyen, Schmitz, Orlov & Ziegler, 2010**

Tropidophorus boehmei T.Q. Nguyen, T.T. Nguyen, A. Schmitz, N.L. Orlov & T. Ziegler, 2010, Zootaxa 2439: 57.

Holotype: VNMN 822.

Type locality: Hoang Lien Mountain, near Ban Khoang, Sa Pa District, Lao Cai Province, northern Vietnam, 1,200–1,300 m a.s.l.

English name: Boehme's Water Skink

Vietnamese name: Than lan tai boe-me

Distribution: This species (Fig. 4a) is currently known only from Hoang Lien Mountain in Sa Pa and Van Ban districts, Lao Cai Province, Vietnam.

Serpentes

Colubridae

***Calamaria gialaiensis* Ziegler, Nguyen & Nguyen, 2008**

Calamaria gialaiensis T. Ziegler, S.V. Nguyen & T.Q. Nguyen, 2008, Current Herpetol., 27(2): 72.

Holotype: IEBR A.0714.

Type locality: Kon Ka Kinh, K Bang District, Gia Lai Province, Vietnam, 1300 m a.s.l.

English name: Gialai Reed Snake.

Vietnamese name: Ran mai gam gia lai.

Distribution: This species (Fig. 4b) is currently known only from Gia Lai Province, Vietnam.

***Calamaria sangi* Nguyen, Koch & Ziegler, 2010 (2009)**

Calamaria sangi T.Q. Nguyen, A. Koch & T. Ziegler, 2010 "2009", Hamadryad 34(1): 2.

Holotype: IEBR 360.

Type locality: Mang Canh Commune, Kon Plong District, Kon Tum Province, Vietnam, 1,200 m a.s.l.

English name: Sang's Reed Snake.

Vietnamese name: Ran mai gam sang.

Distribution: This species is currently known only from Vietnam.

***Colubroelaps nguyenvansangi* Orlov, Kharin, Ananjeva, Nguyen & Nguyen, 2009**

Colubroelaps nguyenvansangi N.L. Orlov, V.E. Kharin, N.B. Ananjeva, T.T. Nguyen & T.Q. Nguyen, 2009, Russ. J- Herpetol. 16(3): 235.

Holotype: ZISP/IEBR 25682.

Type locality: Loc Bac Forest Enterprise, Lam Dong Province, Vietnam, ca. 720 m a.s.l.

English name: Nguyenvansang's Snake.

Vietnamese name: Ran nguyen van sang.

Distribution: The second record of this species was reported by N. Poyarkov from Bu Gia Map National Park, Binh Phuoc Province (Fig. 5). Therefore *Colubroelaps nguyenvansangi* is currently known from Lam Dong and Binh Phuoc provinces, Vietnam.

***Lycodon ruhstrati abditus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, 2009**

Lycodon ruhstrati abditus G. Vogel, P. David, O.S.G. Pauwels, M. Sumontha, G. Norval, R. Hendrix, T.N. Vu & T. Ziegler, 2009, Tropical Zoology 22(2): 144.

Holotype: ZFMK 86451.

Type locality: U Bo region, Phong Nha – Ke Bang National Park, Quang Binh Province, Vietnam.

English name: Hidden Mountain Wolf Snake.

Vietnamese name: Ran khuyet an.

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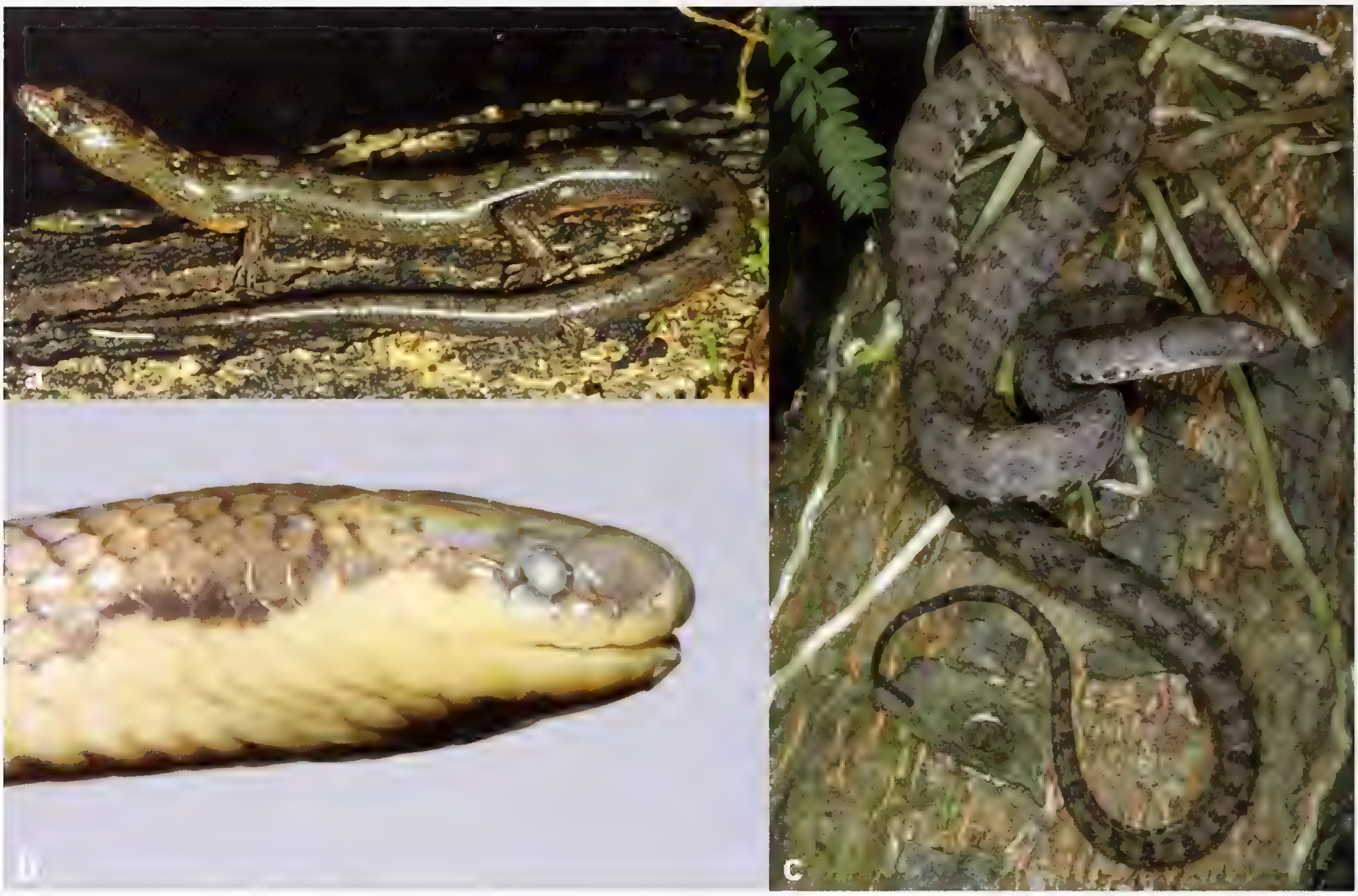

Fig. 4. a) *Tropidophorus boehmei* from Lao Cai Province, Photo T.T. Nguyen; b) Portrait of preserved *Calamaria gialaiensis* from Gia Lai Province, Photo T. Ziegler; and c) *Protobothrops trungkhanhensis* from Cao Bang Province, Photo T.T. Nguyen.

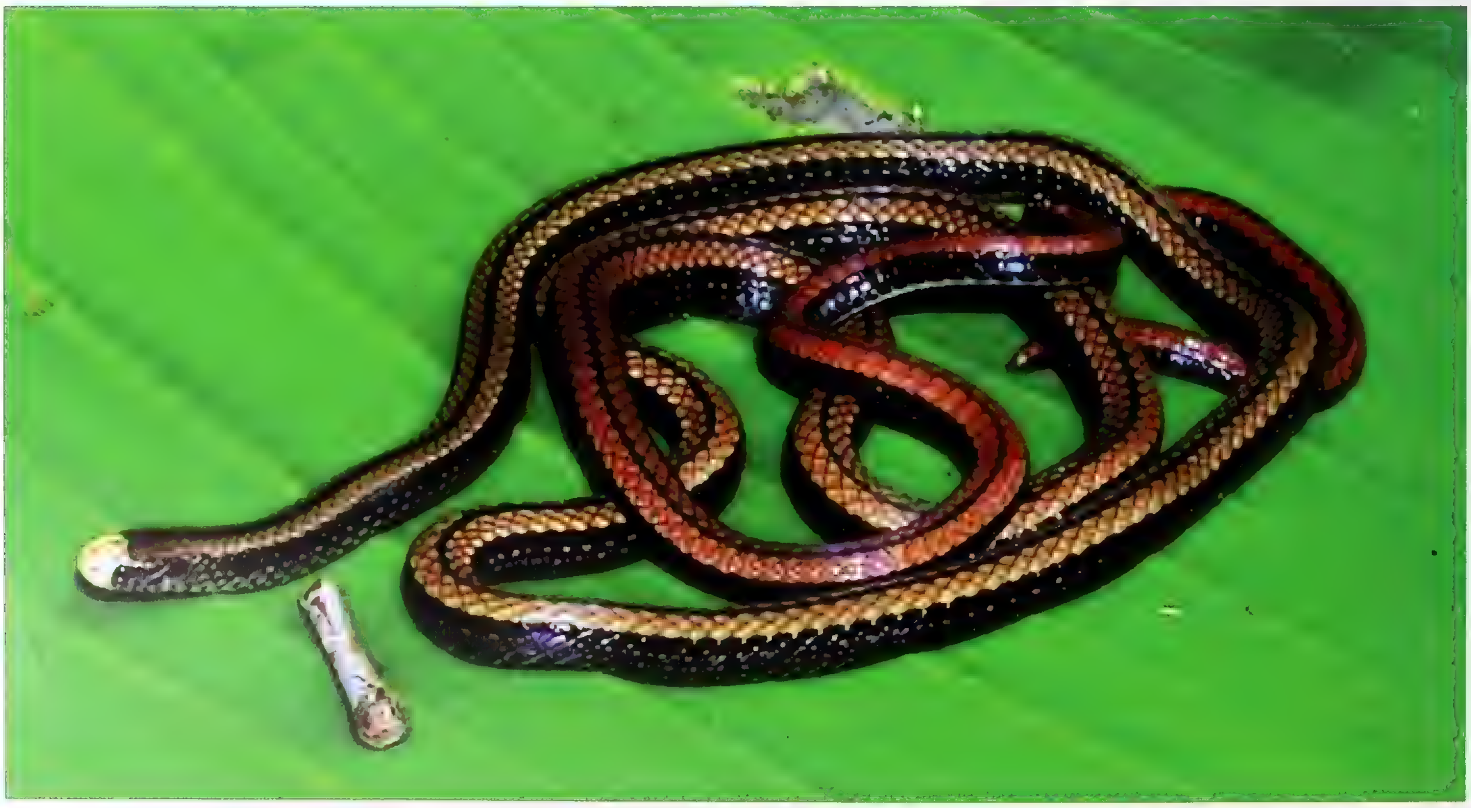

Fig. 5. *Colubroelaps nguyenvansangi* from Binh Phuoc Province, Photo N. Poyarkov.

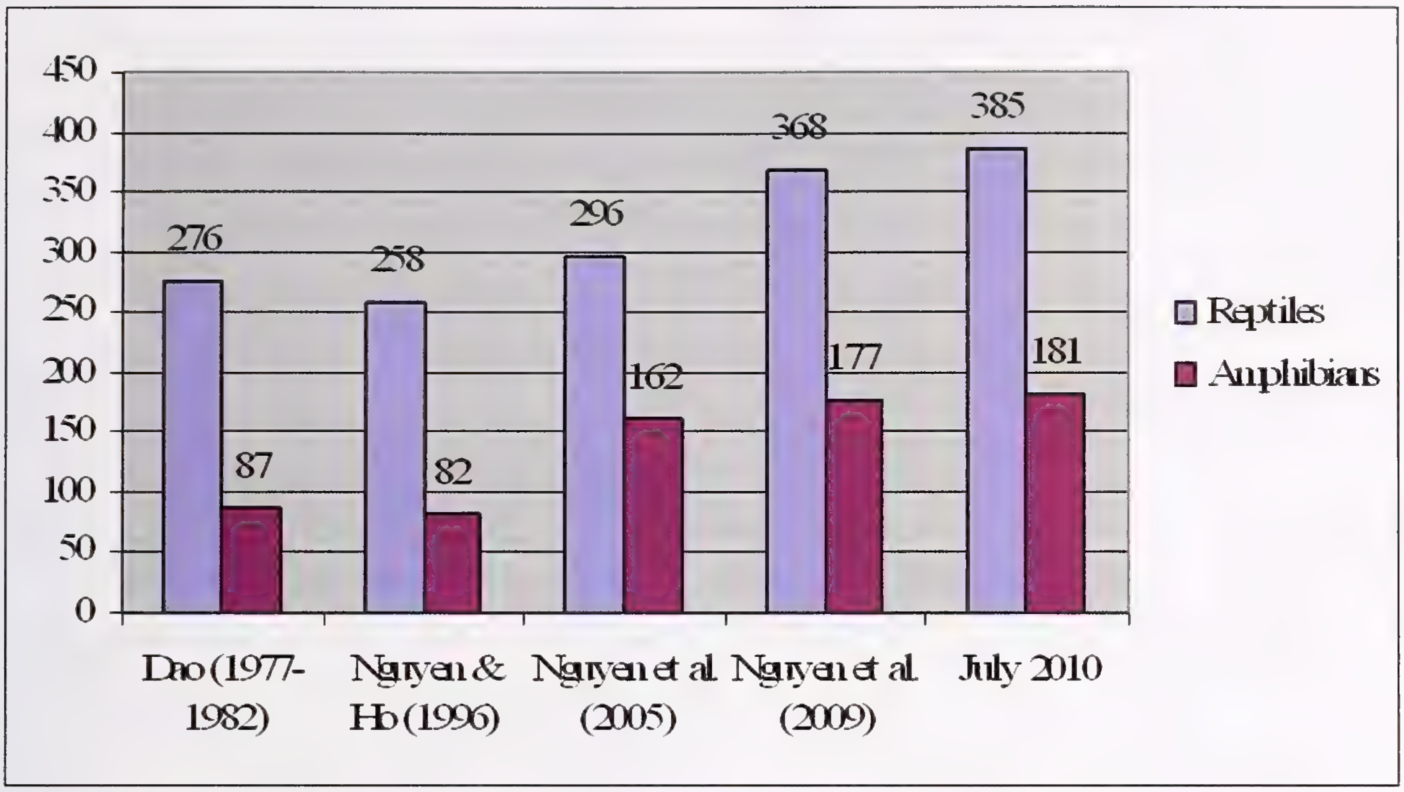

Fig. 6. Species diversity of the herpetofauna of Vietnam.

Distribution: This subspecies is currently known from Quang Binh and Vinh Phuc provinces in Vietnam, and from Fujian, Anhui, Zhejiang, Guangdong, Yunnan, Sichuan and Gansu provinces in China. Because it has often been confused with other taxa, its range is probably much wider, both in northern Vietnam and China (probably also present in Guangxi Province).

Viperidae

Protobothrops trungkhanhensis **Orlov, Ryabov & Nguyen, 2009**

Protobothrops trungkhanhensis N.L. Orlov, S.A. Ryabov & T.T. Nguyen, 2009, Russ. J. Herpetol. 16(1): 71.

Holotype: ZISP 25351.

Type locality: Trung Khanh Nature Reserve, Trung Khanh District, Cao Bang Province, Vietnam, 600 m a.s.l.

English name: Trungkhanh Pitviper.

Vietnamese name: Ran luc trung khanh.

Distribution: This species (Fig. 4c) is currently known only from the type locality.

DISCUSSION

After the publication of the "Herpetofauna of Vietnam" by Nguyen et al. (2009) 20 new amphibian and reptilian species, one new subspecies, and a new snake genus have been described from Vietnam by June 2010. Among them there were three new amphibians (1 Megophryidae, 1 Ranidae, 1 Rhacophoridae) and 18 new reptilian taxa (2 Agamidae, 9 Gekkonidae, 2 Scincidae, 4 Colubridae, and 1 Viperidae). In contrast, two species which were listed as valid and occurring in Vietnam in Nguyen et al. (2009) were synonymized meanwhile: *Gekko ulikovskii* Darevsky & Orlov, 1994 was regarded as a junior synonym of *Gekko badenii* Szczerbak & Nekrasova, 1994 by Nguyen et al. (2010d) and the specimen previously identified as *Pseudocalotes floweri* from Kon Tum Province was re-identified as *P. ziegleri* by Hallermann et al. (2010). Most of the recent species' discoveries affected lizards, with geckos clearly being the predominant group. In addition to these new species descriptions, three new country records were published after the book of Nguyen et al. (2009): one amphibian species, the megophryid anuran *Leptobrachium promustache*, the scincid lizard *Scincella monticola*, and the colubrid snake *Amphiesmoides ornaticeps* (Bain et al. 2009b, Nguyen et al. 2010a, b).

The results of this paper clearly exemplify that even after the comprehensive book provided by Nguyen et al.

(2009) much research is needed to describe Vietnam's rich herpetodiversity. In particular because not only cryptic or inconspicuous species were discovered and formally described in the past months, but also striking and colourful species like *Cnemaspis psychedelica* (Grismer et al. 2010) or even new genera, as was recently shown by the description of *Colubroelaps* (Orlov et al. 2009a). Currently, the herpetofauna of Vietnam comprises 181 species of amphibians and 385 species of reptiles (Fig. 6). However, diversity research and species inventories are only the first steps, which must be followed by investigations of the natural history and specific adaptations, which finally are prerequisites for adequate conservation measures.

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The distinction between family-series and class-series nomina in zoological nomenclature, with emphasis on the nomina created by Batsch (1788, 1789) and on the higher nomenclature of turtles

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Abstract. The *Code* only regulates the scientific names or *nomina* of zoological taxa from the rank subspecies to the rank superfamily, but not those of taxa at ranks above the latter (class-series nomina). It is shown here that its current Rules are somewhat ambiguous regarding the availability of family-series nomina and the distinction between the latter and class-series nomina, and it is again suggested that it should be improved in this respect. It should cover the whole nomenclatural hierarchy in zoology, which requires to expand it in order to incorporate Rules for the nomenclature of higher taxa. A detailed analysis is devoted to the poorly known work of Batsch (1788, 1789), and it is shown that 17 family-series nomina, 16 of which have remained unnoticed until now, are available and should replace the homonymous junior nomina currently considered valid in zootaxonomy. Particular attention is given to the higher nomenclature of turtles, and it is shown that the nomen *TESTUDINES* Batsch, 1788 is a family-series, not a class-series nomen. This nomen is therefore the valid one, as *TESTUDINIDAE* Batsch, 1788, of the family including the genus *Testudo* Linnaeus, 1758, but cannot apply to the order of turtles, tortoises and terrapins.

Key words. Zoological nomenclature, *Code*, availability, class, family, Batsch, turtles, *TESTUDINES*, *TESTUDINIDAE*.

ABBREVIATIONS AND PRINTING CONVENTIONS

In this paper, "ICZN" designates the International Commission on Zoological Nomenclature and "the *Code*" the edition currently in force of the *International Code of Zoological Nomenclature* (Anonymous 1999). For reasons explained in details elsewhere (Dubois 2000, 2006a), some terms of the *Code* are here substituted by other terms, as follows (in the order of their first appearance in the text, indicated there by an asterisk*): *nomen* (plural *nomina*) for "scientific name" (Dubois 2000); *nominal-series* for "groups of names" (Dubois 2000), with four such series ("groups") being discussed here: the *species-*, *genus-*, *family-* and *class-series* (Dubois 2000); *anoplonym* for a "nomenclaturally unavailable name" (Dubois 2000); *sozonym* for a nomen that has had a universal or significant use in non-systematic literature after 31 December 1899 (Dubois 2005a–b); *distagmonym* for a nomen that has not had such a use (Dubois 2005a–b); *onomatophore* for "type" or "name-bearing type" (Simpson 1940); *nucleogenus* (plural *nucleogenera*) for "type genus" (Dubois 2005b); *nucleospecies* for "type species" (Dubois 2005b); *monophory* for "monotypy" (Dubois 2005b); *neonym* for "new replacement name" or "*nomen novum*" (Dubois 2000); *autoneonym* for a neonym being an "unjustified emendation" (Dubois 2000); *archaeonym* for the nomen replaced by a neonym (Dubois 2005a); *hyponymous* for "nominotypical" (Dubois 2006c). The nomina belonging to the species-series and genus-series are printed, as usual, in lower case *italics*, whereas nomina of higher-ranked taxa are printed in small capitals, with the following distinction: family-series nomina are in *ITALICS*, whereas class-series nomina are in **BOLD**. Anoplonyms are printed "between quotation marks".

FAMILY-SERIES AND CLASS-SERIES NOMENCLATURE IN ZOOLOGY

The *Code* regulates the *nomina** of zoological taxa from the rank subspecies to the rank superfamily, but not those of taxa at ranks above the latter. Therefore the use and al-

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location of nomina of taxa referred to the higher ranks of zoological nomenclature (order, class, phylum, etc.) are left to the freedom and opinions of individual zoologists, as no Rules exist in the *Code* for their availability, allocation to taxa and validity, the three basic steps of the nomenclatural process (Dubois 2005a–c, 2006a).

The nomina covered by the *Code* are distributed in three *nominal-series**: the *species-**, *genus-** and *family-series**. Any nomen, to be recognized as nomenclaturally available, must first be explicitly or implicitly referred to one of these nominal-series. No difficulty usually arises regarding the allocation of nomina to the species- and genus-series, but, in some cases, problems may be encountered to know whether a given nomen belongs in the family-series, and thus is governed by the nomenclatural Rules of the *Code*, or to a rank above the family-series, therefore in the *class-series** and thus is outside the Rules of the *Code*.

The *Code* is not fully clear regarding the conditions of availability of family-series nomina. Only two conditions are clear for all nomina, concerning the stem of the nomen and the reference to a suprageneric taxon. Article 11.7.1.1 states that, to be available in its original publication, a family-series nomen must "*be a noun in the nominative plural formed from the stem of an available generic name*", which is then its *nucleogenus** (type-genus). Therefore, any higher taxon nomen *not* based on an available generic nomen is unavailable for a family-series nomen, but may under certain conditions be available for a class-series nomen. Article 11.7.1.2 adds that the new nomen must "*be clearly used as a scientific name to denote a suprageneric taxon and not merely as a plural noun or adjective referring to the members of a genus*". Therefore, the explicit use of the rank family, or of another traditional rank of the family-series (subfamily, superfamily, tribe, subtribe, etc.), is not required for availability of nomina in the family-series. Two additional clear conditions, applying only to nomina published after 1999, are given in Articles 16.1 (the nomen "*must be explicitly indicated as intentionally new*") and 16.2 (the nomen "*must be accompanied by citation of the name of the type genus*"). According to Article 11.7.1.1, before 2000, the type-genus may be indicated "*either by express reference to the generic name or by reference to its stem*", i.e., by *implicit etymological designation* (Dubois 1984).

Three conditions are unclear in the current *Code* regarding the status of new family-series nomina: (C1) the date; (C2) the requirement for validity of the nomen of the nucleogenus; and (C3) the distinction between family-series and class-series nomina.

(C1) No starting date is given in the *Code* for the use of family-series nomina in zoological nomenclature. However, the rank family and related ones (superfamily, subfamily, tribe, subtribe, etc.) were not recognized by Linnaeus (1758, 1761, 1764, 1766, 1767), although this author made use of no less than seven ranks above the rank genus (Dubois 2007). Some authors of the 18th century used the ranks family and tribe, but not always for taxa above the rank genus and below the rank order, with family as a rank above tribe (Dubois 2006a). For example, some authors (e.g., De Geer 1778; Goeze & Donndorff 1797) used family as a rank below the rank genus, whereas others, including some quite recently, used tribe as a rank above the rank order (e.g., Scopoli 1777; de Blainville 1816; Huene 1952) or below the rank order but above the rank family (e.g., Oken 1821, 1833; Fitzinger 1826, 1843; Swainson 1835; Hogg 1841; Bonaparte 1845; de Blainville 1847; Stannius 1856). In zoological taxonomy, the first authors that are traditionally credited with the creation of family-series nomina for taxa above the rank genus are authors who published their works in the early 19th century: e.g., Lamarck (1801), Latreille (1802, 1824, 1825), Oppel (1811a–b), Rafinesque-Schmaltz (1814a–d), Rafinesque (1815), Vieillot (1816), Fischer (1817), Goldfuss (1820), Gray (1825) or Vigors (1825). However, a few authors in the second half of the 18th century already used the rank family for taxa at ranks between genus and order. This is the case of Batsch (1788, 1789), in a rather poorly known work discussed in detail below. Inasmuch as the familial nomina created by these authors were clearly based on the stems of available generic nomina considered valid by these authors, there is no reason for not crediting these authors with the creation of these familial nomina, even if this was ignored by most subsequent authors until now (Dubois 2010: 25).

(C2) Regarding the requirement for validity of the generic nomen used as stem (nucleogenus), Article 11.7.1.1 states that "*the generic name must be a name then used as valid in the new family-group taxon [Arts. 63, 64] (use of the stem alone in forming the name is accepted as evidence that the author used the generic name as valid in the new family-group taxon unless there is evidence to the contrary)*". There are several questions with this unclear formulation. First, what does "*then*" mean in this context? This word would have a clear sense only if it meant "in the work where the new family-series nomen is created", but then why not write it in full words? If it meant "at the period of this work", this would be difficult to apply, first because it is unclear how long the period to be considered should be (preferably it seems that it should not include more than ten or 20 years around the creation of the new family-series nomen), and second because at any given period of taxonomy the same nomen may be accepted as valid by part of the authors then active, and invalid by others, as will be illustrated below with the example of the nomina *Lacerta* Linnaeus, 1758 and *LACERTAE* Batsch, 1788. Furthermore, the words "*used as valid in the new family-group taxon*" show that this condition cannot apply to works published *before* the creation of the latter taxon! Therefore, this part of Article 11.7.1.1 would be made clearer by choosing between the two following formulations: (F1) "*the generic nomen must be used as valid in the new family-group taxon in the work where its nomen is created*"; (F2) "*the generic nomen must be used as valid by all active taxonomists in the 10 years before and after creation of the new family-group nomen*" (or another span). Until this choice is made by the ICZN, this Article is not fully operational, as will be exemplified below. The French version of Article 11.7.1.1 in the current *Code* is not strictly equivalent to its English version, which is problematic as these two texts are deemed to be "*equivalent in force and meaning*" (Anonymous 1999: xiii). As a matter of fact, the French version of this Article ignores the term "*then*" ("*alors*"). In the previous edition of the *Code* (Anonymous 1985: 25), Article 11(f)(i)(1) wrote "*then used as valid for a genus contained in that family-group taxon*". These elements suggest that formulation (F1) above corresponds to the real meaning of this article, and we follow this interpretation below.

(C3) Regarding the distinction between family-series and class-series nomina, it is unambiguous in the *Code* only in the case of suprageneric nomina that are *not* based on available generic nomina, which are unavailable in the family-series, but may be available in the class-series, at least in some cases (see below). But what is the status of nomina based on the stem of available generic nomina created for taxa at ranks clearly above the family-series (order, class, etc.), or for taxa of unusual ranks, not clearly referable to the family- or class-series (such as phalanx, cohort, gens, etc.), or for taxa of unspecified ranks? The *Code* does not provide any clue for decision in such cases, all the more that, as reminded above, the explicit use of the rank family, or of another rank of the family-series, is not required for availability of nomina in the family-series. A few clear situations exist: (1) when a nomen is created for a taxon that is explicitly originally referred to a rank higher than superfamily, or than order, class or another rank traditionally referred for the class-series in zoology, whatever this rank is, such a nomen belongs in the class-series; (2) in contrast, when a nomen is created for a suprageneric taxon of rank lower than superfamily or than any other traditional rank in the family-series (family, subfamily, tribe, etc.), and is based on the stem of a nucleogenus, it belongs in the family-series. But whenever a nomen is proposed for a taxon of any rank above the rank genus, and without clear hierarchical relationships with other taxa of ranks unambiguously referable either to the family- or to the class-series, it may be treated either as a class-series nomen (this is the case for example of all suprageneric nomina created by Linnaeus: see Dubois 2007) or as a family-series nomen. In such cases, the etymology of the nomen may be a help for the decision: if the nomen is based on the stem of an available generic nomen, it may be treated as a family-series nomen, otherwise as a class-series nomen.

Another matter ignored by the *Code* is what could be called the *consistency problem*. In some publications of the 18th, 19th and even 20th centuries, some authors were not consistent regarding the mode of formation of their new familial nomina: some were based on the stem of available generic nomina, whereas others were not, being descriptive or geographical terms, terms based on the names of persons, etc. In such cases, the nomina of the first category could be accepted as available both as family-series and class-series nomina, but those of the second category can be considered available only in the class-series. However, a choice has to be made between these two nominal-series for *all* the nomina created together with the same rank, as it is not logical and conceivable to admit that the same author, in the same publication, created both family-series and class-series nomina for taxa of same rank (for details, see Dubois 2008b). Dubois (2006a: 178) proposed that, in such cases, for reasons of *consistency* in the taxonomic hierarchy, all these nomina be referred to the family-series, but that those which are incorrectly formed (not being based on available generic nomina, or formed through addition of a complex suffix unacceptable as a family-series suffix according to the *Code*), be considered nomenclaturally unavailable. These are of two kinds (Dubois 2006a: 178): *arhizonyms* are family-series nomina not based on generic nomina, and *caconyms* are family-series nomina based on generic nomina but with a complex suffix (such as *-forma*, *-morpha*, etc.). Examples of arhizonyms include "*BATRACINIA*", "*GYMNODERMIA*" and "*PHRYNACINIA*", coined by Rafinesque (1815) for taxa of ranks family or subfamily, along with available family-series nomina like *HYLARINIA*, *RANARINIA* and *TRITONIA*. Examples of caconyms include "*RANIFORMES*", "*HYLAEFORMES*", "*BUFONIFORMES*" and "*PIPAEFORMES*", coined by Duméril & Bibron (1841) for taxa of rank family, along with available family-series nomina like *CÉCILIOÏDES*, *SALAMANDRIDES*, *AMPHIUMIDES* and *PROTÉIDES*.

In his study of class-series nomenclature in zoology, Dubois (2006a: 228), after a detailed discussion of the problems mentioned above and others, proposed two new Rules to clarify this situation and to distinguish between family-series and class-series nomina in a simple, objective and automatic manner:

"*(R4)* ***Allocation of nomina to the family-series or to the class-series****. Whenever a single new suprageneric nomen of a given taxonomic rank was established in a publication, this nomen must be referred to the family-series if both following conditions are fulfilled: (A) it was proposed for a taxon of a rank usual within the family-series or of an unusual rank but clearly presented as being hierarchically subordinate to a usual rank of that series although above the genus; and (B) it was coined by addition of a simple suffix denoting the plural to the stem of an available genus-series nomen. In all other cases, the nomen must be referred to the class-series. Whenever several new suprageneric nomina of the same rank were established in a publication, they must all be referred to the same nominal-series; if they were treated heterogeneously with regard to the criteria above, they must follow the Rule of Taxonomic Consistency (R5).*

(R5) ***Rule of Taxonomic Consistency.*** *All suprageneric nomina created in the same publication for taxa that were afforded the same taxonomic rank must be referred to the same nominal-series. In case of conflict between their allocation to nominal-series according to Rule (R4), the family-series takes precedence over the class-series, and nomina that, being incorrectly formed (arhizonyms or caconyms), cannot be considered as belonging to that series, must be treated as nomenclaturally unavailable (anoplonyms*).*"

These proposed Rules should be studied carefully by the ICZN and incorporated into the *Code*, or others Rules should be proposed, but until this is done, ambiguity will exist and decisions regarding the status of some nomina of higher taxa will remain unclear, and will have to rely on arbitrary decisions on the part of some zoologists, as will now be shown.

In what follows, these general questions will be concretely studied in one zoological group: we will examine the status of the nomina used by the authors until now for (1) the order of reptiles including the turtles and (2) the family of turtles including the genus *Testudo* Linnaeus, 1758.

THE HIGHER NOMENCLATURE OF TURTLES

Despite various works dealing with it, the higher nomenclature of turtles is not yet stabilized. The nomenclatural chaos is clearly emphasized by the use of different and incompatible nomenclatures over very short periods of times, not only by different authors, but sometimes by the same one (e.g., Vetter 2002, 2004; Vetter & van Dijk 2006). The last publications in this respect, by Rhodin et al. (2008, 2009), are not reliable references, as they display ignorance of several basic nomenclatural Rules of the *Code*. For example, they do not follow the *Code*'s Principle of Coordination for superfamilies, which are credited to authors and dates different from those of their *hyponymous** families (e.g., *KINOSTERNIDAE* Agassiz, 1857 and *KINOSTERNOIDEA* Joyce, Parham & Gauthier, 2004) and sometimes given incorrect endings (*TRIONYCHIA* Hummel, 1929). An important nomenclatural flaw, discussed in detail below, is to refer the same nomen (*TESTUDINES* Batsch, 1788) both to the family- and the class-series.

Table 1 (in Appendix 1) provides a survey of various nomina, with their authors and dates when they were specified, that have been used until now by a number of zoologists for the order of turtles and the family including the genus *Testudo* Linnaeus, 1758.

Several problems can be identified in this table. First, although the family including the genus *Testudo* has almost always been known as *TESTUDINIDAE*, the author and date of the latter nomen has not been consensual. Some authors (e.g., Hunt 1958: 150; Iverson 1992: 3; Xianrui 1994: 4) have credited a nomen "Testudines" to Linnaeus (1758: 194, 198). However, it is fully clear that, in this and other works of Linnaeus, the term *Testudines* was a plural noun referring to the members of the genus *Testudo*, not a family-series or class-series nomen (Article 11.7.1.2; Bour & Dubois 1985). This is stressed by the fact that Linnaeus (1758: 198–199) also mentioned this word as *Testudine* and *Testudinibus*. Others have credited the familial nomen *TESTUDINIDAE* to Gray (1825), until Bour & Dubois (1985) drew the attention to the fact that the nomen *TESTUDINES*, coined by Batsch (1788: 437) for a family including the single genus *Testudo* Linnaeus, 1758, was doubtless available in the family-series, where it has priority over all subsequent nomina coined on the basis of the stem of this generic nomen (including *TESTUDIA* Rafinesque-Schmaltz, 1814c, a nomen ignored by most authors until now). Following the *Code*, this nomen must simply be emended to *TESTUDINIDAE* Batsch, 1788 if used for a taxon of rank family, to *TESTUDINOIDEA* Batsch, 1788 for a taxon of rank superfamily, *TESTUDININAE* Batsch, 1788 for a subfamily, *TESTUDININI* Batsch, 1788 for a tribe and *TESTUDININA* Batsch, 1788 for a subtribe.

Still more confusion has been exhibited by the authors regarding the nomen of the order of turtles. The nomen **TESTUDINES** was used for this purpose, credited either to Linnaeus (1758) or to Batsch (1788), which is incorrect in both cases for the reasons given above (the former being a generic nomen in the plural, the latter a family-series nomen). The first valid creation of a nomen **TESTUDINES** for an order was by Wagler (1830: 130, 133), but this is subsequent to the other nomina discussed below. As a matter of fact, three other nomina were also widely used for the order, **CHELONII**, **CHELONIA** and **TESTUDINATA**.

Both **Chelonii** and **Chelonia** are just subsequent latinizations of **Chéloniens** Brongniart, 1800a. The spelling **Chelonia** was first used by Ross & Macartney (and not Macartney alone, as wrongly stated by Loveridge 1957 or Romer 1966) in their 1802 translation of the work of Cuvier (1800). This latinization was posterior to that in **Chelonii** by Latreille (1800), used by many subsequent authors in the 19th century (Bour & Dubois 1985: 79) and resurrected by Bour (1981). Although the *Code* provides no guidelines for the authorship and date of class-series nomina, for reasons discussed in detail by Dubois (2006a, 2009), by simple consistency and parallelism with the Rules of the *Code* concerning family-series and genus-series nomina, it is justified to credit a class-series nomen published first in a non-latinized form to the author of this original nomen, so in this case to Brongniart (1800a). The spelling **Chelonii** being anterior to **Chelonia**, and the latter being open to confusion because of hemihomonymy (Starobogatov 1991) with the generic nomen *Chelonia* Brongniart, 1800b, the use of **Chelonii** was supported by Bour (1981) and Bour & Dubois (1985), who noted that this nomen had priority over **Testudinata**, an ordinal nomen coined by Oppel (1811b). In conclusion, Bour & Dubois (1985) proposed to use the nomen **Chelonii** Brongniart, 1800a for the order of turtles, a suggestion adopted by various subsequent authors (see Table 1).

As the *Code* provides no Rules or even guidelines for class-series nomenclature, this suggestion was based on the use of the Principle of *Onomatophores** (so-called "Principle of Typification") in a way similar to its use in the three lower nominal-series recognized by the *Code*, a method explicitly presented by Dubois (1984). However, as was later shown by Dubois (2004, 2005a–b, 2006a–b, 2009; Dubois & Ohler 2009), because no Principle of Coordination is in force in class-series nomenclature, such a practice does not allow unambiguous allocation of a class-series nomen to a taxon as soon as several hierarchically subordinated taxa have the same onomatophore, so that more complete Rules had to be devised (Dubois 2006a). For the precise allocation of nomina to higher taxa, this system uses both the originally included genera or *conucleogenera* of the newly established taxon, and the genera originally expressly excluded from it, its *alienogenera*. Until these proposed Rules, or others, are incorporated into the *Code* in order to regulate class-series nomenclature, the latter will remain chaotic and left to "freedom" and "opinions" of individual zoologists, which will be a permanent nuisance for proper and unambiguous communication among all biologists.

This problem is made worse by the ambiguity, discussed above, regarding the distinction between class-series and family-series nomina in the *Code*. Although Batsch (1788) had clearly referred his new taxon *TESTUDINES* to the rank family, there is nothing in the *Code* that imposes to refer this nomen to the family-series, all the more that Batsch (1788, 1789) was not consistent in his use of etymology for his familial nomina, some only being based on the stems of generic nomina he considered valid (see below).

Because of this ambiguity of the *Code*, it would be possible to refer the nomen *TESTUDINES* Batsch, 1788 either to the family-series (which clearly has our preference) or to the class-series. But it is fully unacceptable and impossible to refer it to *both*! This would be similar to accepting that a genus-series nomen, such as *Ranoidea* Tschudi, 1838 for example, can be considered available both as the nomen of a genus and of a superfamily! This is however what has been done by Fritz & Havaš (2006, 2007), followed by Vetter & van Dijk (2006) and Rhodin et al. (2008, 2009), who recognized, in the same classification, an order TESTUDINES Batsch, 1788 and a family *TESTUDINIDAE* Batsch, 1788, although both nomina are based on the one and single appearance of the nomen *TESTUDINES* in page 437 of Batsch (1788)! The fact that such incredible nomenclatural treatments can be accepted as valid by several contemporaneous taxonomists and periodicals points to the poor interest granted by many colleagues nowadays to nomenclatural Rules and to the chaotic situation created in zoological nomenclature by the incompleteness and ambiguity of the *Code*.

This exemplary case prompted us to undertake a detailed and complete survey of all suprageneric nomina created by Batsch (1788, 1789), which fully exemplifies these problems and allows to propose solutions to them.

BATSCH'S (1788, 1789) SUPRAGENERIC NOMINA IN ZOOLOGY

Batsch (1788, 1789) was one of the authors who, in the late 18th century, proposed a comprehensive classification of the animal kingdom and tried to improve the scheme of Linnaeus (1758, 1766, 1767) in this respect. In this classification, he used four ranks above the rank genus: family, order, class and an upper unnamed rank that we treat here for more simplicity as "superclass". This classification is summarized here in our Table 2 (in Appendix 1).

Batsch (1788) was the first author to divide the animal kingdom in two main groups, his "superclasses" **Ossea** and **Crustacea**, which exactly correspond to the distinction between "*animaux à vertèbres*" and "*animaux sans vertèbres*" first proposed by Lamarck in his lectures (which were not published until 1801), and which Cuvier (1800) was the first author to formally name in a publication as **Vertébrés (Vertebrata)** and **Invertébrés (Invertebrata)**. Although Batsch's (1788)

Ossea has priority over **Vertebrata**, it would be inappropriate to replace the latter, which has been used millions of times in the scientific literature and therefore qualifies as a *sozonym**, by the former, which has been ignored and which is therefore a *distagmonym** (Dubois 2005a: 86, 2005b: 412).

In his **Ossea**, Batsch (1788) recognized four classes, **Mammalia**, **Aves**, **Amphibia** and **Pisces**, whereas in his **Crustacea** he recognized two classes, **Insecta** and **Vermes**. Although the nomina of these six classes are identical to those of the six zoological classes of Linnaeus (1758, 1766, 1767), their content is not always exactly the same. For example, Batsch (1789) removed from his **Vermes** the genus *Myxine* Linnaeus, 1758 placed in this classis by Linnaeus, and which is in fact a chordate. Therefore, the nomina used by Batsch for these classes should be credited to him, not to Linnaeus. They are junior homonyms of Linnaeus' identical nomina (see Dubois 2006a).

All genera in Batsch (1788, 1789) are referred to families. Families are referred to orders and then to the class only in one class (**Mammalia**). The nomina of the orders of mammals also are in part borrowed from Linnaeus, but here also sometimes with a slightly different content, which requires to consider them as distinct, junior homonymous nomina. In the other five classes, the only rank used above genus is that of family. Because the rank family is expressly used by Batsch, is situated in the nomenclatural hierarchy above the rank genus and below the ranks class and order (when available), and because some at least of these nomina are coined by addition of an ending indicating plural to the stem of an available generic nomen considered valid by Batsch (1788, 1789), we hereby consider the nomina of Batsch's "families" to be indeed family-series nomina, some of which only are nomenclaturally available.

The available family-series nomina in Batsch (1788, 1789), that appear in Table 2, are the 17 familial nomina in his work based on available generic nomina listed by him as valid among the genera of the family. This is for example the case of *Testudines* Batsch, 1788, a taxon expressly mentioned as including the genus *Testudo* Linnaeus, 1758.

As shown in Table 2, there are two categories of unavailable family-series nomina in Batsch (1788, 1789). The first one consists of arhizonyms, i.e., family-series that were not based on any then available zoological generic nomen. The second one consists of nomina that were indeed based on then available zoological generic nomina, but these nomina not being listed by Batsch (1788, 1789) as valid among the members of the family, being presumably considered invalid synonyms of nomina used by Batsch as valid. As we here adopted the formulation (F1) above of Article 11.7.1.1 of the *Code*, these nomina must be considered as nomenclaturally unavailable, but if interpretation (F2) had to be followed these nomina would have to be treated as available. This small doubt is one of the consequences of the ambiguous writing of Article 11.7.1.1 in the current version of the *Code*.

The *Code* is silent about the nomenclatural status of familial nomina such as those created by Batsch (1788, 1789) but shown above to be unavailable in the family-series. In contrast, under the Rules proposed by Dubois (2006a) for class-series nomenclature, these nomina belong unambiguously in the family-series and are therefore clearly unavailable in the class-series as well, because of the Rule of Taxonomic Consistency presented above.

Except three, all the generic nomina listed by Batsch (1788, 1789) in his classification of the animal kingdom had previously been made available in zoological nomenclature by Linnaeus (1758) and in subsequent publications between 1758 and 1790. The only three exceptions are the nomina *Cylindrus* Batsch, 1789, *Hydrocantharus* Batsch, 1789 and *Turris* Batsch, 1789. The status of these three nomina is discussed below in Appendix 2.

Table 3 (in Appendix 1) lists the 17 familial nomina made nomenclaturally available in zoological nomenclature by Batsch (1788, 1789). Until now, only one (*Testudinidae*) has been credited to Batsch (1788), and the other 16 are traditionally credited to other authors at subsequent dates, but should now be credited to Batsch. This poses no problem of "nomenclatural stability", as none of these 16 familial nomina has to change, the change concerning only their author and date.

The familial nomen *Lacertidae*, that had previously (Dubois 2004; Dubois & Bour 2010) been credited to Batsch (1788), does not appear in Table 3. This is because this nomen could be considered available only under interpretation (F2) of Article 11.7.1.1. The genus *Lacerta* Linnaeus, 1758 was recognized by most authors of the end of the 18th century, but not by Laurenti (1768) who had split it into several genera and had not retained the nomen *Lacerta* for any of them (in contrast for what he had done in other cases, e.g. for *Rana*). He was apparently followed in this by Batsch (1788), who did not recognize or even mention the genus *Lacerta*. As we here adopted interpretation (F1) of Article 11.7.1.1, the family nomen *Lacertidae* cannot be credited to Batsch (1788). It must therefore be credited to the first subsequent author who used a family nomen based on the generic nomen *Lacerta* for a family where the latter generic nomen was considered valid. This happens to be Oppel (1811b: 16).

Establishing the proper nomen for the order of turtles (or "turtles, tortoises and terrapins"), i.e., including all recent turtles as well as a few additional Triassic groups, is beyond the scope of the present paper, and we just provide here a few comments in this respect. As discussed above, the nomen *TESTUDINES* Batsch, 1788, being available in the family-series, is not available in the class-series and cannot be used for an order. Under the nomenclatural Rules proposed by Dubois (2006a), the nomina **CHELONII** Brongniart, 1800a and **TESTUDINATA** Oppel, 1811b are available in the class-series. However, they do not apply to the order of turtles, but to still higher taxa.

Under these Rules, the nomen **CHELONII** Brongniart, 1800a applies to the most inclusive class-series taxon containing the genera *Chelonia* Brongniart, 1800b and *Testudo* Linnaeus, 1758, and excluding the 19 nominal genera referred by Brongniart (1800b) to his orders **BATRACHIA**, **OPHIDIA** and **SAURIA**.

As for the nomen **TESTUDINATA** Oppel, 1811b, it applies to the most inclusive class-series taxon containing the genera *Chelonia* Brongniart, 1800b, *Chelys* Oppel, 1811b, *Emys* Duméril, 1806, *Testudo* Linnaeus, 1758 and *Trionyx* Geoffroy Saint-Hilaire, 1809, and excluding the 48 nominal genera referred by Oppel (1811b) to his orders **SQUAMATA** and **NUDA**.

Oppel (1811b) credited the nomina of his orders **TESTUDINATA** and **NUDA** to Klein (1751), a work which, being anterior to 1758, is not nomenclaturally available. However, Joyce et al. (2004: 998) recently drew the attention to Behn's (1760) translation and adaptation of Klein's (1751) book, which includes all the taxa and nomina of the latter work. These post-1758 nomina would be available, with the authorship "Klein *in* Behn, 1760", if this book was nomenclaturally available, but, for reasons explained in detail in our Appendix 2 below, we consider that it should not be considered so.

Several other class-series nomina applying to turtles and related groups have been published after the works just mentioned. Establishing the class-series taxa to which these nomina apply under Dubois's (2006a) proposed Rules requires a long and detailed survey that would take us far beyond the purpose of the present paper and will be presented elsewhere. For the time being, this work is not urgent, as the phylogenetic relationships among these groups, and with the other tetrapods, are currently highly controversial (e.g., Werneburg & Sánchez-Villagra 2009, and included references), and it will be possible to settle a robust nomenclature of these groups only when some consensus emerges on these questions.

CONCLUSION

The analysis presented above and the examples studied show that the current Rules of the *Code* are ambiguous regarding the allocation of nomina of higher zoological taxa to either the family-series or the class-series of nomina, and regarding the conditions of availability of family-series nomina. These Rules should be improved through modifications of Article 11.7.1.1 as suggested above, and mostly through incorporation of Rules for class-series nomina, as proposed in detail by Dubois (2006a).

A detailed study of all suprageneric nomina in the work of Batsch (1788, 1789) shows that this author proposed many family-series nomina, which belong in three categories: (C1) nomina clearly based on the stems of available generic nomina that were considered valid in this work: such nomina are available in the family-series; (C2) nomina apparently based on the stems of generic nomina nomenclaturally available at that time, but not treated as valid in this work: such nomina are unavailable both in the family-series and in the class-series; (C3) arhizonyms, i.e., nomina not based on the stems of any generic nomen nomenclaturally available at that time: such nomina are also unavailable both in the family-series and in the class-series. Nomina of the categories (C2) and (C3) are definitely unavailable and will never have to be used as valid in zoological nomenclature. But the nomina of category (C1) compete for priority with all other family-series subsequently proposed in zoological nomenclature. It so happens that these 17 nomina are identical with family-series nomina coined later on and based on the same nucleogenera. Therefore they must replace them, which entails no change in the nomina themselves (and therefore no disruption of nomenclatural stability) but only modifications regarding their authors and dates. These changes, listed in Table 3, should be implemented without delay in the respective zoological groups where they belong.

This analysis contributes to a clarification of the higher nomenclature of turtles. The nomen *TESTUDINES* Batsch, 1788 is not a class-series, but a family-series nomen. It cannot be used for the order of turtles, but is the valid nomen, under the spelling *TESTUDINIDAE*, of the family including the genus *Testudo* Linnaeus, 1758 and of all other coordinate taxa as recognized in any given classification. As for the order of turtles, establishing the valid nomen of this taxon and of its superordinate taxa under the Rules proposed by Dubois (2006*a*) is beyond the scope

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of the present paper, but it is shown here that neither **Testudines** Linnaeus, 1758, nor **Testudinata** Klein *in* Behn, 1760, nor **Testudines** Batsch, 1788, nor Chelonii Brongniart, 1800a, nor **Testudinata** Oppel, 1811b apply to this taxon. As long as the *Code* does not provide formal Rules for the nomenclature of class-series taxa, the higher nomenclature of turtles (as well as that of all other zoological groups) will remain a matter of personal or collective tastes, opinions and arbitrary decisions of zootaxonomists. At any rate, whatever Rules or guidelines are followed, it is impossible and unacceptable under any nomenclatural philosophy to accept that the nomen *Testudines* Batsch, 1788 could be available *both* for the order of turtles and for the family including the genus *Testudo* Linnaeus, 1758.

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APPENDIX 1

Table 1. Chronological presentation of the family-series and class-series nomina used in various publications for the order of turtles and for the family including the genus *Testudo* Linnaeus, 1758. The authors and dates are mentioned below only when they were so in the works cited. Nomina connected by the sign ↔ are allelonyms (Dubois 2006a), i.e., alternative nomina proposed or used by an author in the same publication for the same taxon (same content and taxonomic rank), without choosing between them.

Reference	Nomen used for the order (or for a class-series taxon of another rank) of turtles	Nomen used for the family including the genus *Testudo* Linnaeus, 1758
Batsch 1788: 437	–	*Testudines*
Brongniart 1800a: 81	**Chéloniens**	–
Latreille 1800: xi	**Chelonii**	–
Ross & Macartney in Cuvier 1802: tab. 3	**Chelonia**	–
Duméril 1806: 76	**Chelonii**	–
Oppel 1811b: 4, 6	**Testudinata** Klein, 1751	*Amydae*
Rafinesque-Schmaltz 1814c: 66	**Perostia**	*Testudia*
Rafinesque 1815: 74	**Perostia**	*Testudia*
Merrem 1820: 6, 7, 12, 17	**Testudinata** Oppel, 1811	–
Latreille 1825: 91	**Chelonii**	**Cryptopodi**
Gray 1825: 194, 210	**Chelonii** Latreille, 1800	*Testudinidae*
Fitzinger 1826: 5	**Monopnoa** [including tribe **Testudinata** Klein, 1751]	*Testudinoidea*
Ritgen 1828: 269, 270	**Chelonii** ↔ **Sterrichrotes**	**Chersochelones** ↔ **Dysmydae**
Wagler 1828: 861	**Chelynae**	**Tylopodae**
Wagler 1830: 130	**Testudines**	**Hedraeoglossae**
Bonaparte 1831: 63, 68	**Chelonii**	*Testudinidae*
Griffith & Pidgeon 1831: 4, 6	**Chelonia**	–
Gray 1831a: 2	**Testudinata**	*Testudinidae*
Gray 1831b: 3, 7	**Chelonii**	*Testudinidae* Gray, 1825
Duméril & Bibron 1834: 346, 352	**Chéloniens** Brongniart, 1800	"*Chersites*"
Duméril & Bibron 1835: 1	**Chéloniens** Brongniart, 1800	"*Chersites*"
Fitzinger 1835: 107	**Monopnoa**	**Tylopoda**
Fitzinger 1843: 29	**Tylopoda** Wagler, 1828	*Testudines*
Rüppel 1843: 297	**Chelonii**	–
Wiegmann & Ruthe 1843: 166, 168	**Chelonii**	*Chersinae*
Gray 1844: 3	**Chelonia**	*Testudinidae*
Bonaparte 1845: 3	**Chelonii**	*Testudinidae*
Bonaparte 1850: pl.	**Chelonii**	*Testudinidae*
Gray 1855: title page, 1, 4	**Testudinata** Oppel, 1811 ↔ **Chelonia** Gray, 1835 [sic]	*Testudinidae*
Agassiz 1857: 235, 249	**Testudinata** Klein, 1751	*Testudinina* Bonaparte, 1831
Günther 1859: 379	**Chelonii**	–
Peters 1862: 271	**Chelonii**	*Testudinidae*
Strauch 1862: 19, 20	**Chelonia**	*Testudinida*
Günther 1864: x, 1, 3	**Chelonia**	*Testudinidae*
Strauch 1865: 205	–	*Testudinida*
Troschel 1866: 182	**Chelonii**	*Testudinida*
Fitzinger 1867: 85	**Chelonii**	*Chersinae*
Gray 1873: iv, 1	**Testudinata**	*Testudinidae*
Cope 1875: 50, 54	**Testudinata**	*Testudinidae*
Peters 1882: 2	**Chelonii** ↔ **Testudinata**	*Testudinina*
Baur 1887: 96, 101	**Testudinata**	*Testudinidae*
Boulenger 1889: 4, 48	**Chelonia** Brongniart, 1800	*Testudinidae*
Strauch 1890: 9, 10	**Chelonia**	*Testudinida*
Baur 1892: 419, 420	**Testudinata**	*Testudinidae*
Boettger 1893: 2, 3	**Chelonia**	*Testudinidae*
Barboza du Bocage 1895: 1	**Chelonia**	*Testudinidae*
Stejneger 1907: 483, 488	**Testudinata** Oppel, 1811	*Testudinidae*
Siebenrock 1909: 429	**Testudinata** Oppel, 1811	*Testudinidae* Gray 1825
De Rooij 1915: 285, 288	**Chelonia**	*Testudinidae*
Stejneger & Barbour 1917: 113	**Testudinata** Oppel, 1811	*Testudinidae*
Boulenger 1923: 42	**Chelonia**	*Testudinidae*

Reference	Nomen used for the order (or for a class-series taxon of another rank) of turtles	Nomen used for the family including the genus *Testudo* Linnaeus, 1758
Mertens & Müller 1928: 20	TESTUDINATA Oppel, 1811	*TESTUDINIDAE*
Smith 1933: 49, 136	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Freiberg 1938: 7, 9	TESTUDINATA Oppel, 1811	*TESTUDINIDAE* Gray, 1825
Terente'v & Chernov 1949: 88, 95	CHELONIA [in subclass TESTUDINES]	*TESTUDINIDAE*
Smith & Taylor 1950: 12, 27	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Schmidt 1953: 86, 104	CHELONIA	*TESTUDINIDAE*
Bergounioux 1955: 187, 508	CHELONIA [in subclass TESTUDINATA]	*TESTUDINIDAE*
Mertens & Wermuth 1955: 333, 370	TESTUDINES	*TESTUDINIDAE*
Romer 1956: 495, 504	CHELONIA ↔ TESTUDINATA	*TESTUDINIDAE*
Loveridge 1957: 163	TESTUDINATA Oppel, 1811	*TESTUDINIDAE*
Loveridge & Williams 1957: 175, 181	TESTUDINATA	*TESTUDINIDAE* Gray, 1825
Hunt 1958: 150	TESTUDINES Linnaeus, 1758	*TESTUDINIDAE* Gray, 1825
Wermuth & Mertens 1961: 1, 171	TESTUDINES	*TESTUDINIDAE*
Fuhn & Vancea 1961: 157, 158	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Goin & Goin 1962: 73, 254	TESTUDINATA	*TESTUDINIDAE*
Yeh, 1963: 7, 27	CHELONIA	*TESTUDINIDAE*
Romer 1966: 365	CHELONIA Macartney, 1802	*TESTUDINIDAE*
Kuhn 1967: 114	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Pritchard 1967: 27	CHELONIA	*TESTUDINIDAE*
Čkhikvazde 1970: 245	CHELONIA	*TESTUDINIDAE*
Auffenberg 1974: 140	TESTUDINATA Shaw, 1802	*TESTUDINIDAE* Gray, 1825
Gaffney 1975: 423	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Młynarski 1976: 6	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Webb et al. 1978: vii	CHELONIA	*TESTUDINIDAE*
Nutaphand 1979: 13, 55	CHELONIA ↔ TESTUDINES	*TESTUDINIDAE*
Bour 1981: 133	CHELONII	*TESTUDINIDAE* Batsch, 1788
De Broin 1982: 897	CHELONII Brongniart, 1800	*TESTUDINIDAE*
Welch 1982: 206, 207	CHELONIA	*TESTUDINIDAE*
Pritchard & Trebbau 1984: 11, 197	TESTUDINES	*TESTUDINIDAE* Gray, 1825
Bour & Dubois 1985: 78	CHELONII Brongniart, 1800	*TESTUDINIDAE* Batsch, 1788
Alderton 1988: 108	CHELONIA	*TESTUDINIDAE*
Dundee 1989: 403	TESTUDINES	–
Ernst & Barbour 1989: 3, 227	TESTUDINES	*TESTUDINIDAE*
King & Burke 1989: 16, 69	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Gray, 1825
Jiufa & Ting, 1992: 1, 4	TESTUDINATA	*TESTUDINIDAE*
Iverson, 1992: 3,	TESTUDINES Linnaeus, 1758	*TESTUDINIDAE* Batsch, 1788
Zhao & Adler, 1993: 164, 171	TESTUDINES	*TESTUDINIDAE*
David 1994: 16, 18	CHELONII Brongniart, 1800	*TESTUDINIDAE* Batsch, 1788
Xianrui 1994: 4, 62	TESTUDINES Linnaeus, 1758	*TESTUDINIDAE* Gray, 1825
Richard 1999: 85	CHELONII Brongniart, 1800	*TESTUDINIDAE*
Boycott & Bourquin 2000: 32	CHELONIA ↔ TESTUDINES	*TESTUDINIDAE*
De Lapparent de Broin 2001: 166, 187	CHELONII Brongniart, 1800	*TESTUDINIDAE* Batsch, 1788
Noriega et al. 2000: 321	CHELONII	*TESTUDINIDAE*
Kuzmin 2002: 17, 84	TESTUDINES	*TESTUDINIDAE* Batsch, 1788
Vetter 2002: 3, 5	TESTUDINES Linnaeus, 1758	*TESTUDINIDAE* Batsch, 1788
Mickoleit 2004: 282, 294	CHELONIA ↔ TESTUDINES	*TESTUDINIDAE*
Pough et al. 2004: 97, 109	TESTUDINES ↔ CHELONIA	*TESTUDINIDAE*
Vetter 2004: 3, 8	TESTUDINES Linnaeus, 1758	*TESTUDINIDAE* Rafinesque, 1815
Vanni & Nistri 2006: 23	CHELONII Brongniart, 1800	*TESTUDINIDAE* Batsch, 1788
Fritz & Havaš 2006: 10, 122	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Batsch, 1788
Vetter & van Dijk 2006: 3, 8	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Batsch, 1788
Fritz & Havaš 2007: 163, 265	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Batsch, 1788
Pritchard 2007: 46	CHELONII Latreille, 1800 ↔ CHELONIA Macartney, 1802 ↔ TESTUDINES [neither Linnaeus, 1758, nor Batsch, 1788]	–
Abbazzi et al. 2008: 123	CHELONII Brongniart, 1800	*TESTUDINIDAE* Batsch, 1788
Rhodin et al. 2008: 2, 12	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Batsch, 1788
Rhodin et al. 2009: 42, 52	TESTUDINES Batsch, 1788	*TESTUDINIDAE* Batsch, 1788

Table 2. The supraspecific taxa of animals listed in Batsch (1788, 1789). The animals are distributed in two class-series taxa, **Ossea** and **Crustacea**, for which no ranks are given in this book; they are here referred to the rank "superclassis". All other ranks are mentioned expressly in Batsch (1788, 1789). Nomina connected by the sign ↔ are *allelonyms* (Dubois 2006a), i.e., alternative nomina proposed by an author in the same publication for the same taxon (same content, onomatophore and taxonomic rank), without choosing between them. The generic nomina are given here under their original spelling (*protonym*; Dubois 2000), with mention between parenthesis of the subsequent spelling (*aponym*; Dubois 2000) used by Batsch, whenever relevant. All these generic nomina had been created by Linnaeus (1758) or in subsequent works published before those of Batsch, except three, followed here by the sign +, which were made nomenclaturally available by Batsch (1789), and the status of which is discussed below in Appendix 1. This appendix also discusses the status of three post-Linnean generic nomina, followed by the sign ‡, which we consider here nomenclaturally unavailable. The familial nomina created by Batsch (1788, 1789) are of three kinds: (1) a familial nomen underlined in this Table was clearly based on the nomen (also underlined) of a genus expressly referred by Batsch to the familia as a *valid* nomen, which is therefore its nucleogenus (type-genus) by implicit etymological designation (Dubois 1984), thus making this family-series nomen available under Art. 11.7.1.1; (2) a familial nomen followed by an asterisk * can be considered derived from the nomen of a genus traditionally referred to the same taxonomic group, but not used as valid by Batsch, being probably considered a synonym of another nomen; this generic nomen is listed between square brackets, also followed by *, after the list of the valid genera of the family according to Batsch; such a family-series nomen, being based on a generic nomen considered invalid by Batsch, is unavailable under Art. 11.7.1.1, thus shown "between quotation marks"; (3) a familial nomen followed by the sign ° is an *arhizonym* (Dubois 2006a: 178), i.e., cannot be construed as being based on a then available generic nomen and is therefore unavailable under Art. 11.7.1.1, thus also shown "between quotation marks".

"Superclassis" **Ossea** Batsch, 1788: 81.
Classis **Mammalia** Batsch, 1788: 87.
Ordo **Bruta** Batsch, 1788: 103.
Familia "*Colossi*"° Batsch, 1788: 107.
Genera (2): *Elephas* Linnaeus, 1758: 18; *Rhinoceros* Linnaeus, 1758: 19.
Familia "*Cataphracta*"* Batsch, 1788: 107.
Genera (2): *Dasypus* Linnaeus, 1758: 18; *Manis* Linnaeus, 1758: 18. [*Cataphractus** Brisson, 1762: 12–13].
Familia *Bradypoda* Batsch, 1788: 108.
Genera (2): *Bradypus* Linnaeus, 1758: 18; *Myrmecophaga* Linnaeus, 1758: 18.
Ordo **Pecora** Batsch, 1788: 103.
Familia "*Ovina*"* Batsch, 1788: 105.
Genera (2): *Camelus* Linnaeus, 1758: 19; *Capra* Linnaeus, 1758: 19. [*Ovis** Linnaeus, 1758: 19].
Familia *Cervina* Batsch, 1788: 105.
Genera (4): *Antilope* Pallas, 1766b: 232; *Bos* Linnaeus, 1758: 19; *Cervus* Linnaeus, 1758: 19; *Moschus* Linnaeus, 1758: 19.
Ordo **Glires** Batsch, 1788: 103.
Familia *Murina* Batsch, 1788: 115.
Genus (1): *Mus* Linnaeus, 1758: 19.
Familia *Leporina* Batsch, 1788: 115.
Genera (4): *Cavia* Pallas, 1766b: 30; *Lepus* Linnaeus, 1758: 19; *Marmota* Blumenbach, 1779: 79; *Spalax* Gueldenstaedt, 1770: 409.
Familia *Sciurina* Batsch, 1788: 115.
Genera (3): *Dipus* Zimmermann, 1780: 354; *Glis* Brisson, 1762: 13, 113; *Sciurus* Linnaeus, 1758: 19.
Familia *Castorea* Batsch, 1788: 115.
Genera (2): *Castor* Linnaeus, 1758: 19; *Hystrix* Linnaeus, 1758: 19.
Ordo **Primates** Batsch, 1788: 103.
Familia "*Primates*"° Batsch, 1788: 108.
Genera (3): *Homo* Linnaeus, 1758: 18; *Lemur* Linnaeus, 1758: 18; *Simia* Linnaeus, 1758: 18.
Ordo **Ferae** Batsch, 1788: 103.
Familia *Felina* Batsch, 1788: 110.
Genus (1): *Felis* Linnaeus, 1758: 18.
Familia *Canina* Batsch, 1788: 110.
Genera (2): *Canis* Linnaeus, 1758: 18; *Hyaena* Brisson, 1762: 13, 168.
Familia *Ursina* Batsch, 1788: 110.
Genus (1): *Ursus* Linnaeus, 1758: 18.
Familia *Mustelina* Batsch, 1788: 110.
Genera (3): *Lutra* Brisson, 1762: 13, 201; *Mustela* Linnaeus, 1758: 18; *Viverra* Linnaeus, 1758: 18.
Ordo **Belluae** Batsch, 1788: 103.
Familia "*Belluae*"° Batsch, 1788: 105.
Genera (4): *Equus* Linnaeus, 1758: 19; *Hippopotamus* Linnaeus, 1758: 19; *Hydrochoerus* Brisson, 1762: 12, 80 (as *Hydrochaerus*); *Sus* Linnaeus, 1758: 18.
Ordo **Rosores** Batsch, 1788: 103.
Familia *Talpina* Batsch, 1788: 113.
Genera (3): *Erinaceus* Linnaeus, 1758: 18; *Sorex* Linnaeus, 1758: 18; *Talpa* Linnaeus, 1758: 18.
Familia "*Pteropoda*"* Batsch, 1788: 105.
Genus (1): *Vespertilio* Linnaeus, 1758: 18. [*Pteropus** Brisson, 1762: 13, 153].

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Familia "*MARSUPIALES*"* Batsch, 1788: 105.

Genus (1): *Didelphis* Linnaeus, 1758: 18 (as *Didelphys*). ["*Marsupiale*"‡ Edward in Catesby, 1771].

Ordo **PINNIPEDA** Batsch, 1788: 103.

Familia "*PINNIPEDA*"° Batsch, 1788: 116.

Genera (3): *Phoca* Linnaeus, 1758: 18; *Rosmarus* Brünnichius, 1771: 34; *Trichechus* Linnaeus, 1758: 18 (as *Trichecus*).

Ordo **CETACEA** Batsch, 1788: 103.

Familia "*CETACEA*"* Batsch, 1788: 116.

Genera (4): *Balaena* Linnaeus, 1758: 19; *Delphinus* Linnaeus, 1758: 19; *Monodon* Linnaeus, 1758: 19; *Physeter* Linnaeus, 1758: 19. [*Cetus** Brisson, 1762: 225].

Classis **AVES** Batsch, 1788: 88.

Familia "*ANSERES*"* Batsch, 1788: 276.

Genera (11): *Alca* Linnaeus, 1758: 84; *Anas* Linnaeus, 1758: 84; *Colymbus* Linnaeus, 1758: 135; *Diomedea* Linnaeus, 1758: 84; *Larus* Linnaeus, 1758: 84; *Mergus* Linnaeus, 1758: 84; *Pelecanus* Linnaeus, 1758: 84; *Phaeton* Linnaeus, 1758: 84; *Procellaria* Linnaeus, 1758: 84; *Rynchops* Linnaeus, 1758: 138 (as *Rhynchops*); *Sterna* Linnaeus, 1758: 84. [*Anser** Brisson, 1760: 262].

Familia "*GRALLAE*"* Batsch, 1788: 276.

Genera (11): *Ardea* Linnaeus, 1758: 84; *Charadrius* Linnaeus, 1758: 85; *Fulica* Linnaeus, 1758: 84; *Haematopus* Linnaeus, 1758: 85; *Phoenicopterus* Linnaeus, 1758: 84; *Platalea* Linnaeus, 1758: 84; *Rallus* Linnaeus, 1758: 84; *Recurvirostra* Linnaeus, 1758: 84; *Scolopax* Linnaeus, 1758: 84; *Tantalus* Linnaeus, 1758: 84; *Tringa* Linnaeus, 1758: 84. ["*Gralla*"‡ Eberling in Sonnerat, 1777].

Familia *STRUTHIONES* Batsch, 1788: 276.

Genera (3): *Didus* Linnaeus, 1766: 119; *Otis* Linnaeus, 1758: 85; *Struthio* Linnaeus, 1758: 85.

Familia "*TENUIROSTRES*"° Batsch, 1788: 276.

Genera (4): *Certhia* Linnaeus, 1758: 83; *Merops* Linnaeus, 1758: 83; *Trochilus* Linnaeus, 1758: 83; *Upupa* Linnaeus, 1758: 83.

Familia "*CUNEIROSTRES*"° Batsch, 1788: 276.

Genera (2): *Alcedo* Linnaeus, 1758: 83; *Picus* Linnaeus, 1758: 83.

Familia "*GALLINAE*"* Batsch, 1788: 276.

Genera (7): *Columba* Linnaeus, 1758: 85; *Crax* Linnaeus, 1758: 85; *Meleagris* Linnaeus, 1758: 85; *Numida* Linnaeus, 1764: 27; *Pavo* Linnaeus, 1758: 85; *Phasianus* Linnaeus, 1758: 85; *Tetrao* Linnaeus, 1758: 85. [*Gallus** Brisson, 1760: 45].

Familia "*ACCIPITRES*"* Batsch, 1788: 277.

Genera (3): *Falco* Linnaeus, 1758: 83; *Strix* Linnaeus, 1758: 83 (as *Stryx*); *Vultur* Linnaeus, 1758: 83. [*Accipiter** Brisson, 1760: 310].

Familia "*LEVIROSTRES*"° Batsch, 1788: 27.

Genera (4): *Buceros* Linnaeus, 1758: 83; *Crotophaga* Linnaeus, 1758: 83; *Psittacus* Linnaeus, 1758: 83; *Ramphastos* Linnaeus, 1758: 83.

Familia *CORACES* Batsch, 1788: 277 ↔ "*PASSERES*"° Batsch, 1788: 277.

Genera (20): *Alauda* Linnaeus, 1758: 85; *Ampelis* Linnaeus, 1766: 119; *Caprimulgus* Linnaeus, 1758: 85; *Coracias* Linnaeus, 1758: 83; *Corvus* Linnaeus, 1758: 83; *Cuculus* Linnaeus, 1758: 83; *Emberiza* Linnaeus, 1758: 85; *Fringilla* Linnaeus, 1758: 85; *Gracula* Linnaeus, 1758: 83; *Hirundo* Linnaeus, 1758: 85; *Jynx* Linnaeus, 1758: 83 (as *Iynx*); *Lanius* Linnaeus, 1758: 83; *Loxia* Linnaeus, 1758: 85; *Motacilla* Linnaeus, 1758: 85; *Oriolus* Linnaeus, 1766: 117; *Paradisaea* Linnaeus, 1758: 110; *Parus* Linnaeus, 1758: 85; *Sitta* Linnaeus, 1758: 83; *Sturnus* Linnaeus, 1758: 85; *Turdus* Linnaeus, 1758: 85.

Classis **AMPHIBIA** Batsch, 1788: 88.

Familia *TESTUDINES* Batsch, 1788: 437.

Genus (1): *Testudo* Linnaeus, 1758: 196.

Familia "*BATRACHI*"° Batsch, 1788: 437.

Genera (4): *Bufo* Laurenti, 1768: 25; *Hyla* Laurenti, 1768: 32; *Pipa* Laurenti, 1768: 24; *Rana* Linnaeus, 1758: 196.

Familia "*LACERTAE*"* Batsch, 1788: 437.

Genera (13): *Basiliscus* Laurenti, 1768: 50; *Caudiverbera* Laurenti, 1768: 43; *Chamaeleo* Laurenti, 1768: 45 (as *Chamaeleon*); *Cordylus* Laurenti, 1768: 51; *Crocodylus* Laurenti, 1768: 53; *Draco* Linnaeus, 1758: 196; *Gekko* Laurenti, 1768: 43; *Iguana* Laurenti, 1768: 47; *Salamandra* Laurenti, 1768: 41; *Scincus* Laurenti, 1768: 55; *Seps* Laurenti, 1768: 58; *Stellio* Laurenti, 1768: 56; *Triton* Laurenti, 1768: 37. [*Lacerta** Linnaeus, 1758: 196].

Familia "*SERPENTES*"* Batsch, 1788: 437.

Genera (16): *Amphisbaena* Linnaeus, 1758: 196; *Anguis* Linnaeus, 1758: 196; *Aspis* Laurenti, 1768: 105; *Boa* Linnaeus, 1758: 196; *Caecilia* Linnaeus, 1758: 229; *Caudisona* Laurenti, 1768: 92; *Cerastes* Laurenti, 1768: 81; *Cobra* Laurenti, 1768: 103; *Coluber* Linnaeus, 1758: 196; *Constrictor* Laurenti, 1768: 106; *Coronella* Laurenti, 1768: 84; *Dipsas* Laurenti, 1768: 89; *Laticauda* Laurenti, 1768: 109; *Naja* Laurenti, 1768: 90; *Natrix* Laurenti, 1768: 73; *Vipera* Laurenti, 1768: 99. [*Serpens** Garsault, 1764: pl. 667].

Classis **PISCES** Batsch, 1788: 88.

Familia "*MULTIFORI*"° Batsch, 1788: 483.

Genera (3): *Petromyzon* Linnaeus, 1758: 196; *Raja* Linnaeus, 1758: 196; *Squalus* Linnaeus, 1758: 196.

Familia "*MONSTROSI*"° Batsch, 1788: 483.

Genera (2): *Chimaera* Linnaeus, 1758: 196; *Lophius* Linnaeus, 1758: 196.

Familia "*GLOBATI*"° Batsch, 1788: 484.

Genera (3): *Diodon* Linnaeus, 1758: 243; *Ostracion* Linnaeus, 1758: 243; *Tetrodon* Linnaeus, 1758: 243.

Familia "*ARTICULATI*"° Batsch, 1788: 484.

Genera (3): *Fistularia* Linnaeus, 1758: 243; *Pegasus* Linnaeus, 1758: 243; *Syngnathus* Linnaeus, 1758: 243.

Familia "*LORICATI*"° Batsch, 1788: 484.

Genera (4): *Acipenser* Linnaeus, 1758: 196; *Centriscus* Linnaeus, 1758: 243; *Cyclopterus* Linnaeus, 1758: 242; *Loricaria* Linnaeus, 1758: 243.

Familia "*SPECULARES*"° Batsch, 1788: 484.

Genera (7): *Callionymus* Linnaeus, 1758: 242 (as *Callyonimus*); *Cottus* Linnaeus, 1758: 242; *Gobius* Linnaeus, 1758: 242; *Scorpaena* Linnaeus, 1758: 242; *Trachinus* Linnaeus, 1758: 242; *Uranoscopus* Linnaeus, 1758: 242; *Zeus* Linnaeus, 1758: 242.

Familia "*SOLEATI*"* Batsch, 1788: 484.

Genera (3): *Balistes* Linnaeus, 1758: 243; *Chaetodon* Linnaeus, 1758: 242; *Pleuronectes* Linnaeus, 1758: 242. ["*Solea*"‡ Edwards in Catesby, 1771].

Familia "*FERI*"° Batsch, 1788: 485.

Genera (11): *Coryphaena* Linnaeus, 1758: 242; *Esox* Linnaeus, 1758: 243; *Gasterosteus* Linnaeus, 1758: 242; *Labrus* Linnaeus, 1758: 242; *Mullus* Linnaeus, 1758: 243; *Perca* Linnaeus, 1758: 242; *Salmo* Linnaeus, 1758: 243; *Sciaena* Linnaeus, 1758: 242; *Scomber* Linnaeus, 1758: 243; *Sparus* Linnaeus, 1758: 242; *Trigla* Linnaeus, 1758: 243.

Familia "*BRACTEATI*"° Batsch, 1788: 485.

Genera (5): *Clupea* Linnaeus, 1758: 243; *Cyprinus* Linnaeus, 1758: 243; *Exocoetus* Linnaeus, 1758: 243; *Mugil* Linnaeus, 1758: 243; *Polynemus* Linnaeus, 1758: 243.

Familia "*NUDI*"° Batsch, 1788: 485.

Genera (7): *Anarhichas* Linnaeus, 1758: 242; *Blennius* Linnaeus, 1758: 242; *Cobitis* Linnaeus, 1758: 243; *Echeneis* Linnaeus, 1758: 242; *Gadus* Linnaeus, 1758: 242; *Silurus* Linnaeus, 1758: 243; *Xiphias* Linnaeus, 1758: 242.

Familia "*SERPENTINI*"° Batsch, 1788: 485.

Genera (4): *Ammodytes* Linnaeus, 1758: 242; *Gymnotus* Linnaeus, 1758: 242; *Muraena* Linnaeus, 1758: 242; *Trichiurus* Linnaeus, 1758: 242.

"Superclassis" **CRUSTACEA** Batsch, 1788: 84.

Classis **INSECTA** Batsch, 1788: 89.

Familia "*COLEOPTERA*"° Batsch, 1789: 539.

Genera (21): *Attelabus* Linnaeus, 1758: 342; *Buprestis* Linnaeus, 1758: 342; *Byrrhus* Linnaeus, 1766: 537; *Cantharis* Linnaeus, 1758: 342; *Carabus* Linnaeus, 1758: 342; *Cassida* Linnaeus, 1758: 342; *Cerambyx* Linnaeus, 1758: 342; *Chrysomela* Linnaeus, 1758: 342; *Cicindela* Linnaeus, 1758: 342; *Coccinella* Linnaeus, 1758: 342; *Curculio* Linnaeus, 1758: 342; *Dermestes* Linnaeus, 1758: 342; *Elater* Linnaeus, 1758: 342; *Hydrocantharus*+ Batsch, 1789: 550; *Lampyris* Geoffroy, 1762: 165; *Mordella* Linnaeus, 1758: 342; *Necydalis* Linnaeus, 1758: 342; *Nicrophorus* Fabricius, 1775: 71; *Scarabaeus* Linnaeus, 1758: 342; *Silpha* Linnaeus, 1758: 342; *Tenebrio* Linnaeus, 1758: 342.

Familia "*HEMIPTERA*"° Batsch, 1789: 539.

Genera (5): *Blatta* Linnaeus, 1758: 342; *Forficula* Linnaeus, 1758: 342; *Gryllus* Linnaeus, 1758: 342; *Meloe* Linnaeus, 1758: 342; *Staphylinus* Linnaeus, 1758: 342.

Familia "*NEVROPTERA*"° Batsch, 1789: 539.

Genera (7): *Ephemera* Linnaeus, 1758: 343; *Hemerobius* Linnaeus, 1758: 343; *Libellula* Linnaeus, 1758: 543; *Myrmeleon* Linnaeus, 1767: 539 (as *Myrmeleo*); *Panorpa* Linnaeus, 1758: 343; *Phryganea* Linnaeus, 1758: 343; *Raphidia* Linnaeus, 1758: 343.

Familia "*HYMENOPTERA*"° Batsch, 1789: 540.

Genera (9): *Apis* Linnaeus, 1758: 343; *Chrysis* Linnaeus, 1761: xlii; *Cynips* Linnaeus, 1758: 343; *Formica* Linnaeus, 1758: 343; *Ichneumon* Linnaeus, 1758: 343; *Sirex* Linnaeus, 1761: xli; *Sphex* Linnaeus, 1758: 343; *Tenthredo* Linnaeus, 1758: 343; *Vespa* Linnaeus, 1758: 343.

Familia "*DIPTERA*"° Batsch, 1789: 540.

Genera (10): *Asilus* Linnaeus, 1758: 344 (as *Asylus*); *Bombylius* Linnaeus, 1758: 344; *Conops* Linnaeus, 1758: 344; *Culex* Linnaeus, 1758: 344; *Empis* Linnaeus, 1758: 344; *Hippobosca* Linnaeus, 1758: 344; *Musca* Linnaeus, 1758: 344; *Oestrus* Linnaeus, 1758: 344; *Tabanus* Linnaeus, 1758: 344; *Tipula* Linnaeus, 1758: 344.

Familia *CIMICARIA* Batsch, 1789: 540.

Genera (3): *Cimex* Linnaeus, 1758: 343; *Nepa* Linnaeus, 1758: 343; *Notonecta* Linnaeus, 1758: 343.

Familia *CICADINA* Batsch, 1789: 540.

Genera (6): *Aphis* Linnaeus, 1758: 343; *Chermes* Linnaeus, 1758: 343; *Cicada* Linnaeus, 1758: 343; *Coccus* Linnaeus, 1758: 343; *Fulgora* Linnaeus, 1766: 538; *Thrips* Linnaeus, 1758: 343.

Familia "*LEPIDOPTERA*"° Batsch, 1789: 540.

Genera (10): *Alucita* Linnaeus, 1758: 496; *Bombyx* Linnaeus, 1758: 495; *Geometra* Linnaeus, 1758: 496; *Papilio* Linnaeus, 1758: 343; *Phalaena* Linnaeus, 1758: 343; *Pyralis* Linnaeus, 1758: 496; *Sphinx* Linnaeus, 1758: 343 (as *Sphynx*); *Tinea* Linnaeus, 1758: 496; *Tortrix* Linnaeus, 1758: 496; *Zygaena* Fabricius, 1775: 550.

Familia "*HEXAPODA*"° Batsch, 1789: 540.

Genera (4): *Lepisma* Linnaeus, 1758: 344; *Pediculus* Linnaeus, 1758: 344; *Podura* Linnaeus, 1758: 344; *Pulex* Linnaeus, 1758: 344.

Familia "*POLYPODA*"° Batsch, 1789: 540.

Genera (10): *Acarus* Linnaeus, 1758: 344; *Aranea* Linnaeus, 1758: 344; *Cancer* Linnaeus, 1758: 344; *Gammarus* Fabricius, 1775: 418; *Julus* Linnaeus, 1758: 344 (as *Iulus*); *Monoculus* Linnaeus, 1758: 344; *Oniscus* Linnaeus, 1758: 344; *Phalangium* Linnaeus, 1758: 344; *Scolopendra* Linnaeus, 1758: 344; *Scorpio* Linnaeus, 1758: 344.

Classis **VERMES** Batsch, 1788: 89.

Familia "*INTESTINA*"° Batsch, 1789: 664.

Genera (8): *Ascaris* Linnaeus, 1758: 644; *Cucullanus* Müller, 1777: pl. 38 fig. 1–7; *Echinorynchus* Müller, 1776: 214 (as *Echinorhynchus*); *Gordius* Linnaeus, 1758: 644; *Hirudo* Linnaeus, 1758: 644; *Hydatigena* Goeze, 1782: 192; *Taenia* Linnaeus, 1758: 646; *Trichuris* Roederer, 1761: 243.

Familia "*SETIPEDA*"° Batsch, 1789: 664.

Genera (4): *Aphrodita* Linnaeus, 1758: 644; *Lumbricus* Linnaeus, 1758: 644; *Nais* Müller, 1771: 6; *Nereis* Linnaeus, 1758: 644.

Familia "*UBERES*"° Batsch, 1789: 665.

Genera (6): *Argonauta* Linnaeus, 1758: 645; *Clio* Linnaeus, 1767: 1072; *Lernaea* Linnaeus, 1758: 644; *Nautilus* Linnaeus, 1758: 645; *Scyllaea* Linnaeus, 1758: 644; *Sepia* Linnaeus, 1758: 644.

Familia *LIMACINA* Batsch, 1789: 665.

Genera (25): *Aplysia* Linnaeus, 1767: 1072 (as *Laplysia*); *Buccinum* Linnaeus, 1758: 645; *Bulla* Linnaeus, 1758: 645; *Cassis* Scopoli, 1777: 393; *Chiton* Linnaeus, 1758: 645; *Conus* Linnaeus, 1758: 645; *Cylindrus*+ Batsch, 1789: 692; *Cymbium* Mendes da Costa, 1776: 182; *Cypraea* Linnaeus, 1758: 645; *Doris* Linnaeus, 1758: 644; *Fasciola* Linnaeus, 1758: 644; *Haliotis* Linnaeus, 1758: 645; *Helix* Linnaeus, 1758: 645; *Limax* Linnaeus, 1758: 644; *Murex* Linnaeus, 1758: 645; *Nerita* Linnaeus, 1758: 645; *Orthoceras* Bruguière, 1789: xvi; *Patella* Linnaeus, 1758: 645; *Purpura* Bruguière, 1789: xv; *Serpula* Linnaeus, 1758: 645; *Strombus* Linnaeus, 1758: 645; *Tethys* Linnaeus, 1758: 644; *Turbo* Linnaeus, 1758: 645; *Turris*+ Batsch, 1789: 691; *Voluta* Linnaeus, 1758: 645.

Familia "*SYPHONATA*"° Batsch, 1789: 665.

Genera (17): *Anomia* Linnaeus, 1758: 645; *Arca* Linnaeus, 1758: 645; *Ascidia* Linnaeus, 1767: 1072; *Cardium* Linnaeus, 1758: 645; *Chama* Linnaeus, 1758: 645; *Mactra* Linnaeus, 1767: 1073; *Mya* Linnaeus, 1758: 670; *Mytilus* Linnaeus, 1758: 645; *Ostrea* Linnaeus, 1758: 645; *Pecten* Müller, 1776: 248; *Perna* Philipsson, 1788: 20; *Pholas* Linnaeus, 1758: 645; *Pinna* Linnaeus, 1758: 645; *Solen* Linnaeus, 1758: 645; *Spondylus* Linnaeus, 1758: 645; *Tellina* Linnaeus, 1758: 645; *Venus* Linnaeus, 1758: 645.

Familia "*CRISTATA*"° Batsch, 1789: 665.

Genera (6): *Actinia* Pallas, 1766b: 152; *Balanus* Mendes da Costa, 1778: 249; *Holothuria* Linnaeus, 1758: 644; *Lepas* Linnaeus, 1758: 645; *Medusa* Linnaeus, 1758: 644; *Triton* Linnaeus, 1758: 644.

Familia "*CRUSTOSA*"° Batsch, 1789: 665.

Genera (2): *Asterias* Linnaeus, 1758: 644; *Echinus* Linnaeus, 1758: 644.

Familia "*FRONDOSA*"° Batsch, 1789: 665.

Genera (2): *Astrophyton* Schultze, 1760: 53; *Pennatula* Linnaeus, 1758: 646.

Familia "*POLYPINA*"° Batsch, 1789: 666.

Genera (10): *Alcyonium* Linnaeus, 1758: 646; *Eschara* Linnaeus, 1758: 646; *Gorgonia* Linnaeus, 1758: 646; *Hydra* Linnaeus, 1758: 646; *Isis* Linnaeus, 1758: 646; *Madrepora* Linnaeus, 1758: 646; *Millepora* Linnaeus, 1758: 646; *Sertularia* Linnaeus, 1758: 646; *Spongia* Linnaeus, 1759: 1317; *Tubularia* Linnaeus, 1758: 646.

Familia "*FIMBRIATA*"° Batsch, 1789: 666.

Genera (3): *Brachyonus* Pallas, 1766a: 89; *Trichoda* Müller, 1773: 71; *Vorticella* Linnaeus, 1767: 1074.

Familia "*CHAOTICA*"* Batsch, 1789: 666.

Genera (10): *Burfaria* Müller, 1773: 62; *Cercaria* Müller, 1773: 64; *Cyclidium* Müller, 1773: 49; *Enchelis* Müller, 1773: 33; *Gonium* Müller, 1773: 60; *Kolpoda* Müller, 1773: 56; *Monas* Müller, 1773: 25; *Paramaecium* Müller, 1773: 54; *Vibrio* Müller, 1773: 39; *Volvox* Linnaeus, 1758: 646. [*Chaos** Linnaeus, 1767: 1074].

Table 3. The family-series nomina made available in Batsch (1788, 1789), with the authors and dates traditionally credited to them in zootaxonomy. The traditional nomina of families and higher taxa given in the third and last columns are those recognized in the site of the Taxonomicon (http://taxonomicon.taxonomy.nl/). For the only one for which authorship and date are not given in this site, marked by an asterisk*, we give those recognized in the site Wikipedia (http://en.wikipedia.org/wiki/). The publication credited in the Taxonomicon site to "Fischer de Waldheim" is actually signed by the single name "Fischer" and should be cited under this name (Dubois 2008a).

Family nomen appearing in Batsch (1788, 1789)	Nucleogenus	Nomen traditionally used for this family	Protonym of nomen traditionally used for this family	Valid nomen of this family	Traditional higher taxa: phylum, classis, ordo
Bradypoda Batsch, 1788	*Bradypus* Linnaeus, 1758	*Bradypodidae* Gray, 1821	*Bradypidae* Gray, 1821: 304	*Bradypodidae* Batsch, 1788	**Chordata, Mammalia, Pilosa**
Canina Batsch, 1788	*Canis* Linnaeus, 1758	*Canidae* "Fischer de Waldheim", 1817	*Canini* Fischer, 1817: 372	*Canidae* Batsch, 1788	**Chordata, Mammalia, Carnivora**
Castorea Batsch, 1788	*Castor* Linnaeus, 1758	*Castoridae* Hemprich, 1820	*Castorina* Hemprich, 1820: 33	*Castoridae* Batsch, 1788	**Chordata, Mammalia, Rodentia**
Cervina Batsch, 1788	*Cervus* Linnaeus, 1758	*Cervidae* Goldfuss, 1820	*Cervina* Goldfuss, 1820: 374	*Cervidae* Batsch, 1788	**Chordata, Mammalia, Artiodactyla**
Cicadina Batsch, 1789	*Cicada* Linnaeus, 1758	*Cicadidae* Westwood, 1840	*Cicadae* Westwood, 1840: 422	*Cicadidae* Batsch, 1789	**Arthropoda, Insecta, Hemiptera**
Cimicaria Batsch, 1789	*Cimex* Linnaeus, 1758	*Cimicidae* Latreille, 1802	*Cimicides* Latreille, 1802: 240	*Cimicidae* Batsch, 1789	**Arthropoda, Insecta, Hemiptera**
Coraces Batsch, 1788	*Coracias* Linnaeus, 1758	*Coraciidae* Vigors, 1825	*Coraciana* Vigors, 1825: 399	*Coraciidae* Batsch, 1788	**Chordata, Sauropsida, Coraciiformes**
Felina Batsch, 1788	*Felis* Linnaeus, 1758	*Felidae* "Fischer de Waldheim", 1817	*Felini* Fischer, 1817: 372	*Felidae* Batsch, 1788	**Chordata, Mammalia, Carnivora**
Leporina Batsch, 1788	*Lepus* Linnaeus, 1758	*Leporidae* "Fischer de Waldheim", 1817	*Leporini* Fischer, 1817: 372	*Leporidae* Batsch, 1788	**Chordata, Mammalia, Lagomorpha**
Limacina Batsch, 1789	*Limax* Linnaeus, 1758	*Limacidae* Lamarck, 1801	*Limaciers* Lamarck, 1801: 62	*Limacidae* Batsch, 1789	**Mollusca, Gastropoda, Pulmonata**
Murina Batsch, 1788	*Mus* Linnaeus, 1758	*Muridae* Illiger, 1815	*Murina* Illiger, 1815: 46	*Muridae* Batsch, 1788	**Chordata, Mammalia, Rodentia**
Mustelina Batsch, 1788	*Mustela* Linnaeus, 1758	*Mustelidae* "Fischer de Waldheim", 1817	*Mustelini* Fischer, 1817: 372	*Mustelidae* Batsch, 1788	**Chordata, Mammalia, Carnivora**
Sciurina Batsch, 1788	*Sciurus* Linnaeus, 1758	*Sciuridae* "Fischer de Waldheim", 1817	*Sciurii* Fischer, 1817: 372	*Sciuridae* Batsch, 1788	**Chordata, Mammalia, Rodentia**
Struthiones Batsch, 1788	*Struthio* Linnaeus, 1758	*Struthionidae* "Fischer de Waldheim", 1817	*Struthionidae* Vigors, 1825: 402	*Struthionidae* Batsch, 1788	**Chordata, Sauropsida, Struthioniformes**
Talpina Batsch, 1788	*Talpa* Linnaeus, 1758	*Talpidae* "Fischer de Waldheim", 1817	*Talpini* Fischer, 1817: 372	*Talpidae* Batsch, 1788	**Chordata, Mammalia, Erinaceomorpha**
Testudines Batsch, 1788	*Testudo* Linnaeus, 1758	*Testudinidae* Batsch, 1788*	*Testudines* Batsch, 1788: 437	*Testudinidae* Batsch, 1788	**Chordata, Sauropsida, Testudines**
Ursina Batsch, 1788	*Ursus* Linnaeus, 1758	*Ursidae* "Fischer de Waldheim", 1817	*Ursini* Fischer, 1817: 372	*Ursidae* Batsch, 1788	**Chordata, Mammalia, Carnivora**

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APPENDIX 2

THE NOMENCLATURAL STATUS OF A FEW PROBLEMATIC ZOOLOGICAL NOMINA

THE ZOOLOGICAL NOMINA CREATED IN THE BOOK OF BEHN (1760)

Klein (1751) published a comprehensive classification of his "Quadrupedia", i.e., roughly, the tetrapods without the cecilians, snakes, birds and whales. This book in Latin being pre-1758, the nomina it contains are nomenclaturally unavailable. Joyce et al. (2004) pointed out the existence of Behn's (1760) German translation and adaptation of Klein's (1751) book, where all the taxa and nomina of the latter work are reproduced. These post-1758 nomina would be available, with the authorship "Klein *in* Behn, 1760", if this book had to be considered nomenclaturally available, but it should not. The nomenclatural hierarchy used in this book is unclear and inconsistent. It includes the ranks ordo (Ordnung) and familia (Familie), the taxa at these ranks being designated by uninomina (nomina consisting of a single term). The ranks used below the rank Familie are denominated in German Geschlecht, then Art, then Gattung. Considering their hierarchy and content, they could be construed to correspond respectively to the ranks tribe, genus and species, but this would probably be misleading. Each of these ranks can contain a various numbers of unnamed subranks, and the number of terms used to designate taxa is variable, from one to two and more, some of these nomina being plurinominal diagnoses borrowed without change from various pre-1758 works. This work clearly does not comply with the requirement of Article 11.4 of the *Code* for the availability of species-, genus- and family-series nomina. However, this might not preclude considering the class-series nomina in this work, or some of them, as available, since Article 11.4 implicitly states that "*this Article does not apply to the availability of names of taxa above the family group*".

If it was possible to establish objectively where lays the separation between the family-series and the class-series nomenclature in Behn (1760), and if all these nomina were uninomina, it could be possible to recognize as available the class-series nomina proposed in this work, but this is difficult if not impossible.

The nomina of the three orders of "Quadrupedia" recognized in Behn (1760) are plurinomina, as follows: (O1) "*Pilosa et Ungulata (vivipara) sive* "Ζωοτοκα"; (O2) "*Pilosa et Digitata sive sint tota coriacea, sive cataphracta; omnia vivipara*"; (O3) "*Depilata, sive tecta, sive nuda, nequicquam pilosa, omnia ovipara, sive* "Ωοτοκα". Such designations are in fact diagnoses, and cannot qualify as nomina of zoological taxa. They are unavailable in zoological nomenclature. It can be noted that, in the original text of Klein (1751), the same taxa were designated by uninomina ("Ungulata", "Digitata" and "Depilata"), but as this text is pre-Linnaean, these nomina also are unavailable.

In contrast, the nomina of the 13 "families" recognized by Behn (1760) are all uninomina. They are distributed as follows in the three orders: (O1) "Monochelon", "Dichelon", "Trichelon", "Tetrachelon" and "Pentachelon"; (O2) "Didactylon", "Tridactylon", "Tetradactylon", "Pentadactylon" and "Anomalapes" (instead of "Anomalopes" in Klein, 1751); (O3) "Testudinata", "Cataphracta" and "Nuda". Except possibly for one, these nomina are not based on the stems of included nominal genera. "Testudinata" could be construed to be based on the stem of the only included genus of the family, *Testudo* Linnaeus, 1758, but this is highly improbable. The other twelve familial nomina are clearly based on characters that are considered diagnostic for the taxa they designate, and the nomen "Testudinata" can also be understood as based on the Latin adjective *testudinatus*, meaning "of turtle, vaulted, arched". Therefore, all nomina of "families" in Behn (1760) appear to be arhizonyms. Under the Rules of Dubois (2006a), such nomina cannot be accepted as family-series nomina and qualify as class-series nomina. This case is not unique. Other examples were discussed by Dubois (2006a, 2009) and Dubois & Ohler (2009): for example, the nomina of "families" in Ritgen (1828), which are also arhizonyms, must be treated as available class-series nomina.

However, in the case of the new familial nomina appearing in Behn (1760), difficulties would arise if they were to be treated as available class-series nomina. In the system of Dubois (2006a), the allocation of class-series nomina to taxa is made through their included (conucleogenera) and excluded (alienogenera) nominal genera, and to be usable in this respect, conucleogenera and alienogenera must be nomenclaturally available. If all the nomina of taxa just below the rank family in Behn (1760), designating taxa of rank "Geschlecht", were considered to be genus-series nomina, part of them could not be used for taxonomic allocation of their nomina, because they are unavailable in Behn's (1760) work. In his order (O3), corresponding to the traditional amphibians and reptiles, only three generic nomina then available are mentioned as valid nomina: *Testudo* Linnaeus, 1758 for a "Geschlecht" of his family "Testudinata"; *Lacerta* Linnaeus, 1758 for a "Geschlecht" of his family "Nuda"; *Rana* Linnaeus, 1758 for an "Art" of his "Geschlecht" "*Batrachus*" (then an unavailable nomen) of his family "Nuda"; and none in his family "Cataphracta". In order to allocate the nomen "Nuda" to a class-series taxon, one would have to take an arbitrary decision, considering that either the rank "Geschlecht" or the rank "Art" corresponds to the rank genus in the current *Code*. If the rank "Geschlecht" was considered to correspond to the rank genus, and "Art" to the rank species, the nomen "NUDA" would apply, in a modern classification, to the most inclusive taxon including the genus *Lacerta* and excluding the genus *Testudo*. But if the rank "Geschlecht" was considered to correspond to the rank tribe, and "Art" to the rank genus, the nomen "NUDA" would apply, in a modern classification, to the most inclusive taxon including the genus *Rana* and excluding all the mammalian genera, bearing then available Linnaean generic nomina, mentioned by Behn (1760) in his orders (O1) and (O2). Therefore, according to the arbitrary decision taken, the same nomen could apply to widely distinct higher taxa.

Because of these uncertainties, many other examples of which could be given, we here argue that Behn's (1760) should not be considered as an available work in zoological nomenclature, even for class-series nomina. We suggest that this book should be invalidated as a whole by the ICZN, and that all the new nomina it contains should be considered unavailable in zoological nomenclature.

"*Marsupiale*" Edwards in Catesby, 1771

According to Sherborn (1902: 593), there exists a genus *Marsupiale*, based on the following reference: "G. Edwards in M. Catesby, Carol. I. 1771, xxix". Actually this refers to Catesby (1771a: xxix), in "An account…" added by George Edwards, where the binomen *Marsupiale americanum* appears, with a diagnosis. However, this item follows another one entitled *Vulpi affinis americana* and many others where the nomenclature is not consistently binominal. Consequently the ICZN (Anonymous 1954) has suppressed the whole work (Catesby 1771a-b) for nomenclatural purposes, except for the nomina employed by Edwards in accordance with the Linnean system in his "Catalogue of the Animals and Plants" (i.e., Catesby 1771a: 1–2, 1771b: 1–2), usually referred as George Edwards' "Appendix".

"*Solea*" Edwards in Catesby, 1771

According to Sherborn (1902: 593), there exists a genus *Solea*, based on the following reference: "G. Edwards in M. Catesby, Carol. II. 1771, 27". Actually this refers to Catesby (1771b: 27), where appears the combination *Solea lunata et punctata*, with a diagnosis and a plate; however, this is not a binomen, and therefore it has no status in nomenclature. The ICZN (Anonymous 1954) has suppressed the whole work (Catesby 1771a-b) for nomenclatural purposes, except for the nomina employed by Edwards in accordance with the Linnean system in his "Catalogue of the Animals and Plants" (i.e., Catesby 1771a: 1–2, 1771b: 1–2), usually referred as George Edwards' "Appendix". Edwards (in Catesby 1771b: 1) linked this description with the binomen *Pleuronectes lunatus* Linnaeus, 1758.

"*Gralla*" Eberling in Sonnerat, 1777

According to Sherborn (1902: 431), there exists a genus *Gralla*, based on the following reference: "J. P. Ebeling in Sonnerat, Reise Neuguinea, 1777, 31". Actually this refers to Sonnerat (1777: 31 [and 45]), where appears the combinations *gralla parra* and *gralla fulica*. Wieland (2010) admitted the nomenclatural availability of both, which he treated as binomina, and also of the genus *Gralla* Sonnerat, 1777, but with this comment: "*The basic data of this taxon were not entered consulting the original description, but from secondary sources*". On the other hand, *The Richmond Index*, published by the Division of Birds at the National Museum of Natural History, Washington, D.C (Anonymous 2010), states that *Gralla* Ebeling in Sonnerat is not nomenclaturally a valid generic name: "Gralla fulica *p. 45;* Gralla parra *p. 31, Ebeling, in Sonnerat, Reise Neu Guinea, 1777. These have no standing! being simply Ebeling's way of writing Order Grallæ, Genus* Fulica + Parra*!!".* Actually Ebeling (in Sonnerat 1777) put a capital at the start of the generic name of his binomina, but neither at *gralla parra* nor at *gralla fulica*. We follow here *The Richmond Index* statement and do not recognize the nominal genus "*Gralla* Ebeling *in* Sonnerat, 1777".

Cylindrus Batsch, 1789: 692

Three homonymous nominal genera *Cylindrus* are available in zoological nomenclature: *Cylindrus* Batsch, 1789: 692; *Cylindrus* Deshayes, 1824: 236; and *Cylindrus* Fitzinger, 1833: 107.

Cylindrus Batsch, 1789 has apparently been ignored by all authors until now. It was introduced with a diagnosis that makes it nomenclaturally available and that clearly points to marine cone shells.

Cylindrus Deshayes, 1824 is an *autoneonym** (unjustified emendation) of *Cylinder* Denys de Montfort, 1810: 390, a nomen established for a genus of marine cone shells. Its *nucleospecies** (type-species) is *Conus textile* Linnaeus, 1758: 717, by original designation. The original nomen of this genus was preceded in zoological nomenclature by *Cylinder* Voet, 1793 and *Cylinder* Voet, 1806, but both these nomina are unavailable, as published in books that are not consistently binominal. Strangely enough however, the nomen *Cylinder* Denys de Montfort, 1810 is currently not considered valid, but its autoneonym *Cylindrus* Deshayes, 1824 is so, being currently treated as a subgenus of the genus *Conus* Linnaeus, 1758 (e.g., Keen 1971; Pitt et al. 1986).

Cylindrus Fitzinger, 1833 was established with a single valid species included, *Pupa obtusa* Draparnaud, 1805: 63, which is therefore its nucleospecies by original specific *monophory** (monotypy). This generic nomen is currently (e.g., Frank 2006) considered valid for a genus of terrestrial snails.

The current nomenclatural situation concerning the use of the term *Cylindrus* in zoological nomenclature is not compliant with the Rules of the *Code*, for two distinct reasons: (R1) the autoneonym *Cylindrus* Deshayes, 1824 of *Cylinder* Denys de Montfort, 1810 is considered valid instead of its *archaeonym**, although the latter should be so, not being preoccupied by an available homonymous generic nomen; (R2) two homonymous genus-series nomina, *Cylindrus* Deshayes, 1824 and *Cylindrus* Fitzinger, 1833, are currently both considered valid in zoology, although the second one, being a junior homonym of the former, should be considered invalid (even if the former one was not so). The two nomina are listed as valid in several current online databases, but apparently never in the same one: *Cylindrus* Deshayes, 1824 appears as the valid nomen of a subgenus of *Conus* Linnaeus, 1758 in the databases *Catalogue of recent and fossil* Conus *(Alan J. Kohn)* [http://biology.burke.washington.edu/conus/recordview/specieslist_P.html], *The sea shells (Nauka Bulgarie)* [http://theseashells.nauka.bg/Conus_Cylindrus_textile_textile.html] and Hardy's Internet *Guide to marine Gastropods (Eddie Hardy)* [http://jeh-temp.co.uk/Taxon_pages/Family_CONIDAE_CONINAE.shtml], whereas *Cylindrus* Fitzinger, 1833 appears as the valid nomen of a genus of terrestrial snails in the databases *Molluscs of central Europe (Dr. Vollrath Wiese, Cismar, D-23743 Grömitz-Cismar)* [http://www.mollbase.de/list/liste.php], *Animalbase Goettingen* [http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/search] and *Biolib.cz* [http://www.biolib.cz/en/taxon/id18384].

The rediscovery of the nomen *Cylindrus* Batsch, 1789, created for a genus of marine cone shells, allows to clarify this nomenclatural situation. We hereby designate *Conus textile* Linnaeus, 1758 as its nucleospecies (type-species). The nomen *Cylindrus* Batsch, 1789 therefore replaces both *Cylinder* Denys de Montfort, 1810 and *Cylindrus* Deshayes, 1824 as the valid nomen of the subgenus of *Conus* Linnaeus, 1758 including the latter species. As for *Cylindrus* Fitzinger, 1833, it is an invalid junior homonym of both *Cylindrus* Batsch, 1789 and *Cylindrus* Deshayes, 1824 and it must be abandoned.

The homonymy between *Cylindrus* Deshayes, 1824 and *Cylindrus* Fitzinger, 1833 was pointed out by Kennard (1942), in a work that seems to have been overlooked by most subsequent authors. This author rightly concluded that the nomen *Cylindrus* Fitzinger, 1833 is invalid, and pointed to the existence of its senior objective synonym *Cochlopupa* Jan, 1830: 5. The nucleospecies of this nominal genus is *Pupa obtusa* Draparnaud 1805 by original specific monophory. The single species currently referred to the genus *Cylindrus* Fitzinger, 1833 and known as *Cylindrus obtusus*, must therefore bear the nomen *Cochlopupa obtusa* (Draparnaud, 1805).

***Hydrocantharus* Batsch, 1789: 550**

The nomen *Hydrocantharus* Batsch, 1789, created for an aquatic beetle (dytiscid) is identical to several pre-1758 uses of the same nomen, which are nomenclaturally unavailable. For the same genus, Linnaeus (1758: 342) used the nomen *Dytiscus*. In this genus, he listed (p. 411–413) 15 nominal species, among which Latreille (1810: 426) designated *Dytiscus marginalis* Linnaeus, 1758: 411 as nucleospecies. We hereby designate the same nominal species as nucleospecies (type-species) of *Hydrocantharus* Batsch, 1789, which therefore becomes an invalid junior objective synonym of *Dytiscus* Linnaeus, 1758.

***Turris* Batsch, 1789: 691**

A generic nomen *Turris* was created for a gastropod genus by Statius Müller (1766: 129), but this nomen is unavailable as having been published in a book invalidated by the ICZN (Anonymous 1964) as not applying the principle of binominal nomenclature. A homonymous nomen *Turris* was later created by Röding (1798: 123) also for a gastropod genus, and this nomen is currently considered valid. However, the present rediscovery of *Turris* Batsch, 1789 makes *Turris* Röding, 1798 its invalid junior synonym.

As reckoned by Winckworth (1945), the nucleospecies of *Turris* Röding, 1798 is *Murex babylonius* Linnaeus, 1758: 753, by subsequent designation of Bucquoy et al. (1883: 86). In order not to upset nomenclatural stability, we hereby designate *Murex babylonius* Linnaeus, 1758 as nucleospecies (type-species) of *Turris* Batsch, 1789. The latter must now replace its junior objective synonym *Turris* Röding, 1798 as the valid nomen of the genus.

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An addition to the East African herpetofauna: the first record of *Tarentola annularis relicta* (Squamata: Gekkonidae) in Uganda

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Abstract. This is the first record of a member of the genus *Tarentola* from Uganda. Population of *Tarentola annularis relicta* was found in Ubbi village on the South-Western foot of Mt. Otzi in northern Uganda, close to the border with Sudan. Brief comments on extraordinary biogeographical affinities of the area and characterization of the Mt. Otzi environments are provided.

Key words: *Tarentola*, Uganda, East Africa, Mt. Otzi, new geographic record.

INTRODUCTION

In their account of the East African reptiles, Spawls et al. (2004) listed 55 species of geckoes in 11 genera for East Africa including Tanzania, Kenya, Uganda, Rwanda and Burundi. Although biogeographically, the East African realm includes also parts of South Sudan and Ethiopia, we follow the above mentioned political delimitation of East Africa used throughout literature for practical reasons. During a short survey of the Mt. Otzi area in the very North of Uganda on 9.X.2006, we collected specimens of geckoes, that did not match any known East African genus. Specimens were collected on buildings of the village school in Ubbi, a small settlement at the South-Western foot of Mt. Otzi. Upon collection, the animals were photographed and released at the original collection site.

The Ubbi village (03°35’07”N, 31°49’42”E, elevation of 690 m a.s.l.) is surrounded by a mosaic of farmland, small rocky hillocks covered by bushy vegetation and numerous rocky outcrops devoid of vegetation (Fig. 1a). The area is situated in the Southern Sudanian savanna zone, the natural vegetation of which is mostly tree and shrub moist savanna. The dominant geomorphological feature of the area is the Mt. Otzi massif steeply rising above surrounding landscape. The Mt. Otzi located on the Western bank of the Nile River has an undulating top plateau with several emergent rocky peaks reaching a maximum elevation of 1565 m. Its slopes are covered by bush, while its upper parts are covered by a mosaic of highland bush, moist forest and farmland (Fig. 1b). The remaining forest patches are mostly degraded by logging and clearing for agriculture and thus characterized by relatively open canopy (Fig. 1c). The area south of the Mt. Otzi is dominated by palm- and other moist-savanna types (Fig. 1d).

Tarentola specimens

The geckoes were assigned to the genus *Tarentola* according to absence of claws on digits 1, 2 and 5 and presence of claws on digits 3 and 4 (as seen in Figs 2a–b). The only *Tarentola* species occurring thus far in the South-East of the genus range is *Tarentola annularis* (Geoffroy, 1809), in which two subspecies are recognized (Joger 1984). The nominotypic *Tarentola annularis annularis* (Geoffroy, 1809) occurs throughout the Saharan region, whereas *Tarentola annularis relicta* Joger, 1984 is known only from two disjunct areas – the Nile valley in the very south of Sudan and Mora in the North Cameroon south of the Lake Chad. Two confirmed Sudan localities include Juba (type locality of the subspecies) and Nimule (Joger 1984).

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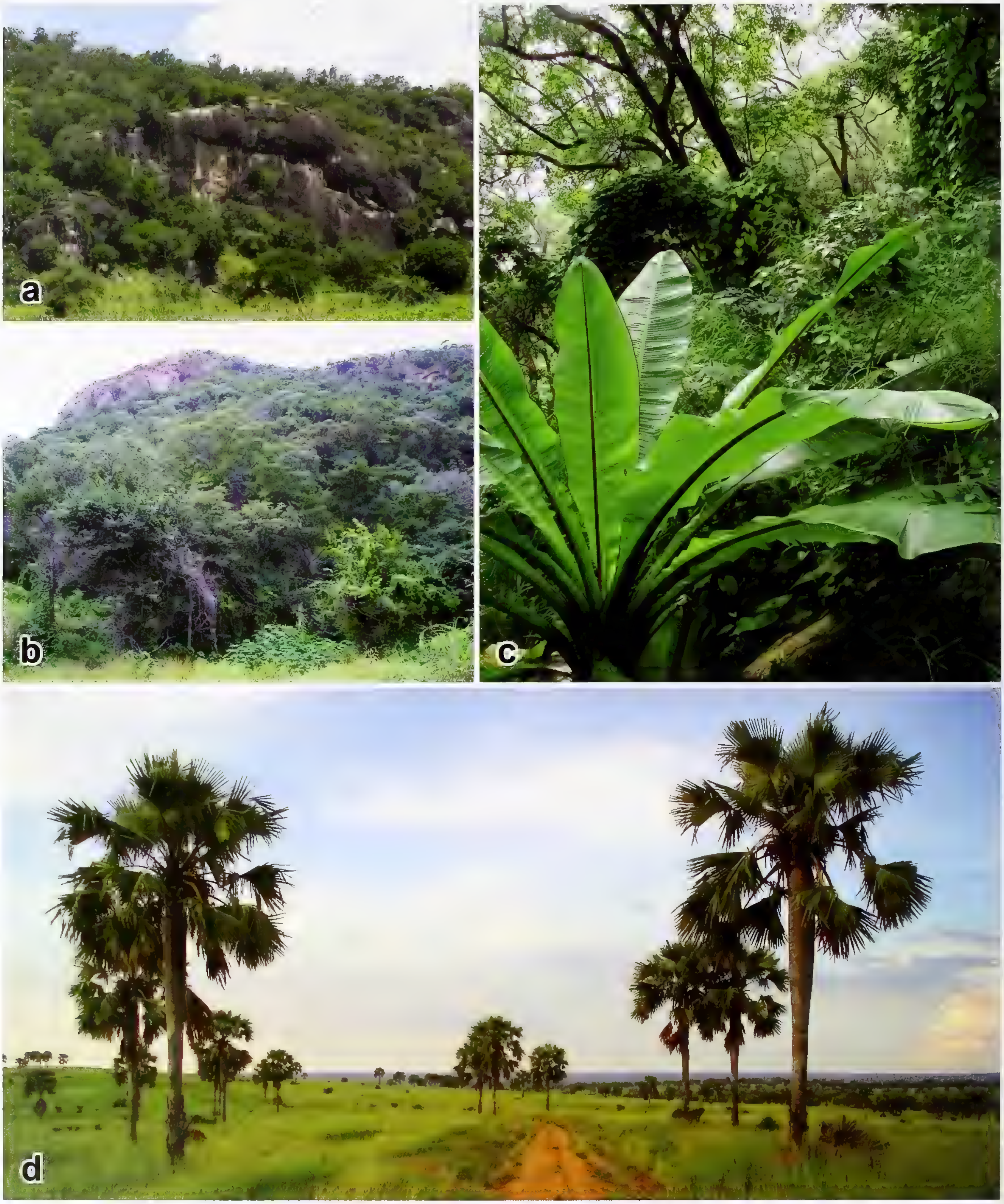

Fig. 1. Landscape and vegetation of the Mt. Otzi and adjacent areas. **Fig. 1a.** Rocky outcrops in Ubbi village on the foot of Mt. Otzi. Photograph A. D. Mihalca. **Fig. 1b.** Forest patch on the Mt. Otzi top plateau with an emergent rocky peak in the background. Photograph M. Jirků. **Fig. 1c.** Interior of the Mt. Otzi forest showing relatively open canopy and distinct Afromontane floristic element, the false banana of the genus *Ensete* in the foreground. Photograph M. Jirků. **Fig. 1d.** Palm savanna south of the Mt. Otzi region in the Murchinson Falls NP, Uganda. Photograph M. Jirků.

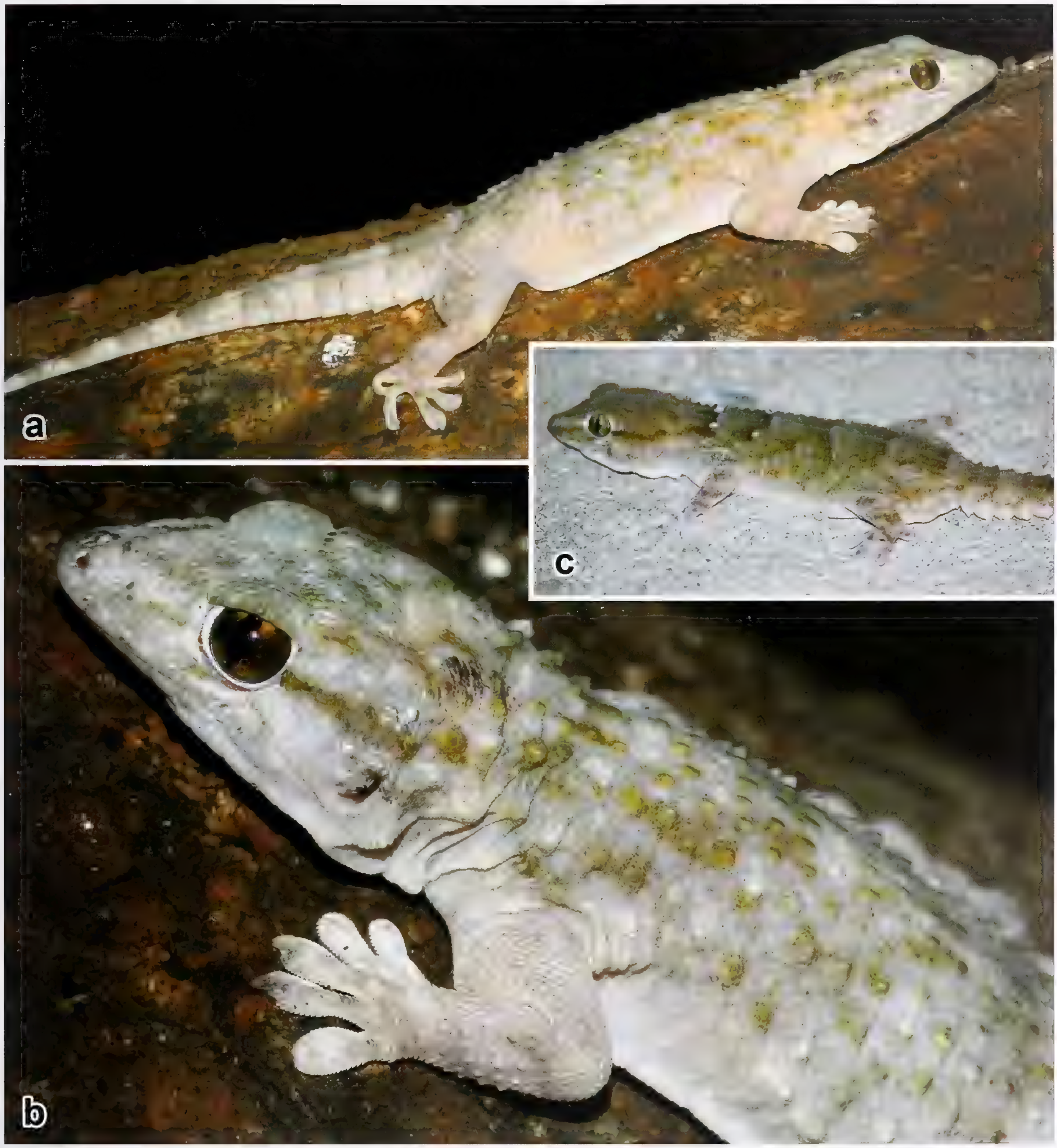

Fig. 2. *Tarentola annularis*. **Fig. 2a.** Adult specimen of *Tarentola annularis relicta* from Ubbi, Uganda. Photograph D. Modrý. **Fig. 2b.** Close-up of adult specimen of *Tarentola annularis relicta* from Ubbi, Uganda. Note the bright red trombiculid mites localized mainly around eye. Photograph D. Modrý. **Fig. 2c.** Adult specimen of *Tarentola annularis annularis* from Awash NP, Ethiopia. Note the four distinct white, dark-rimmed scapular flecks. Photograph P. Necas.

Apart from details in scaling patterns, *T. a. relicta* can be readily distinguished visually by an absence of four white, dark-rimmed scapular flecks typical for the nominotypic subspecies (compare Figs 2a–b with Fig. 2c). Based on coloration pattern, the specimens we collected in Uganda can be assigned to the subspecies *T. a. relicta*. All observed specimens were pale-grey colored with orange to orange-brown blotches on dorsum of the head and body with intervening irregularly distributed faint whitish flecks devoid of any dark margin, whereas the tail possessed just faint grayish transversal bands (Figs 2a–b). As far as we are aware, the Figs 2a–b are the first published color photographs of live *T. a. relicta*.

BIOGEOGRAPHICAL CONSEQUENCES

To our best knowledge, the presented record of *Tarentola* in Uganda is the first record of the genus in the East African region as defined above. The genus *Tarentola* comprises 20 species distributed throughout the dry regions of the Mediterranean, Middle East, some Atlantic archipelagos (e.g. Canary and Cape Verde Islands) and African mainland north of the savanna and forest zones (see Joger 1984 for review). Three additional species are known from the West Indies (Díaz & Hedges 2008, Joger 1984). The African-mainland part of the genus geographic range, i.e. Saharan region, comprises a total of six species (including *Tarentola chazaliae*, still treated by some authors as the only representative of the monotypic genus *Geckonia* – see Carranza et al. 2002) the speciation of which seems to reflect the relatively recent aridification of the Sahara desert region, which was gradually colonized from its rather mesic margins by ancestors of extant species since mid Oligocene. In general, the southern distribution limit of *Tarentola* spp. in African mainland is delimited by an interference zone between the southern margin of the arid Sahel belt and moist savanna and forest equatorial zones.

To date, the southernmost confirmed locality of *Tarentola* has been the record of *T. a. relicta* from Nimule (03°35’33”N, 32°04’14”E), on the Sudanian side of the Sudan-Uganda border. The southern records of *T. a. relicta* in Sudan and Uganda document an intrusion of Saharan faunistic element into the relatively humid equatorial region which is dominated by moist savanna approximately from 9°30’N southwards. Presence of the reptile species associated with arid habitats here, deep in the savanna zone might be facilitated by a presence of an extensive network of huge rocky outcrops and ridges following Aswa fault, which extend into this region from far north-west and of which the Mt. Otzi is a magnificent southernmost outpost. It is possible, that these exposed rocky formations, largely devoid of vegetation, might serve as refuges for Saharan taxa that normally would not occur thus far south in the otherwise relatively humid region. Farther to the south from the Mt. Otzi region, the landscape is dominated by gently undulating plains covered by various moist-savanna types (Fig. 1d) where presence of *Tarentola* seems unlikely due to lack of suitable habitats.

Interestingly, the Mt. Otzi region is the easternmost known locality of a remarkable West-African savanna element, the ball python *Python regius*, which was collected in the vicinity of Moyo (3°39’14”N, 31°43’22”E), just 13 km to the north-west from the Ubbi village reported here to be (together with Nimule) the southernmost locality of *Tarentola*.

Apart from the two outstanding herpeto-faunistic elements, *P. regius* and *T. a. relicta*, representatives of the West African and Saharan realm(s) respectively, the region is mostly inhabited by East-African herpetofauna as reflected by distribution maps provided by Spawls et al. (2004). In addition, there is a relict population of eastern chimpanzee *Pan troglodytes schweinfurthii* on the Mt. Otzi (Caldecott & Miles 2005), which together with colobus monkey *Colobus guereza* (pers. obs.) in the Otzi forest show clear faunistic affinity to the Guineo-Congolian rainforest block. Finally, a presence of false bananas of the genus *Ensete* (pers. obs., Fig. 1c) in the Otzi forest suggests also presence of Afromontane elements in the area. In conclusion, the Mt. Otzi region deserves further attention as a potential biogeographical match point, where East- and West-African (savanna), Saharan (desert), Central-African (forest-savanna) and possibly Afromontane biotas meet at one place.

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The taxonomic status of *Hyperolius spatzi* Ahl, 1931 and *Hyperolius nitidulus* Peters, 1875 (Amphibia: Anura: Hyperoliidae)*

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* this paper is dedicated to Prof. Dr. Wolfgang Böhme, who's 1978 paper on the herpetology of Senegal induced our investigations presented herein.

Abstract. We herein re-investigate the taxonomic status of *Hyperolius nitidulus* Peters, 1875 and *H. spatzi* Ahl, 1931 by means of morphology, vocalization and genetic data. Both taxa are morphologically distinct, have different advertisement calls and differ genetically from each other by 5.1–5.6% sequence divergence in the investigated 16S rRNA gene. Based on these data we resurrect *H. spatzi* as a valid species and designate a lectotype for it. Both species occur in savannas of western Africa. *Hyperolius spatzi* is restricted to Senegambia and thus far known from Senegal and The Gambia. Its occurrence in Guinea Bissau and southern Mauritania seems likely. *Hyperolius nitidulus* ranges from Guinea and Mali eastwards into Nigeria and Cameroon. Records from the driest savannas in north-eastern Nigerian, Cameroon and the Central African Republic are doubtful and may actually refer to *H. pallidus* Mertens, 1940.

Key Words. Bioacoustics, biogeography, genetics, morphology, savanna, West Africa.

INTRODUCTION

Many species of the diverse African reedfrog genus *Hyperolius* Rapp, 1842 exhibit very variable color patterns (Schiøtz 1971, 1975, 1999). Some of these color variations are age and sex specific (Schiøtz 1967, Veith et al. 2009). As these frogs offer comparatively few other species specific morphological characters, this variability caused considerable taxonomic confusion in the past and resulted in the description of many taxa which are now regarded as synonyms (Frost 2010). One author in particular, Ernst Ahl, contributed to this chaos by describing many new species (e.g. Ahl 1931a, b), most of which proved to be invalid (Laurent 1961, Frost 2010). As the in-depth studies of Schiøtz (1967, 1971, 1975) and others have shown, color and advertisement calls are the most reliable characters for identification of these species. Unfortunately, alcohol preserved *Hyperolius* specimens quickly loose color (and do not call). Therefore it is often difficult, if not impossible, to evaluate the status of older museum vouchers. Reliable locality data may be of help in some cases where taxa show allopatric distributions and/or different habitat requirements.

One group of savanna dwelling reedfrogs proved to be especially variable and consequently taxonomically complicated: the *Hyperolius marmoratus/viridiflavus* complex (Laurent 1951b, c, 1981; Schiøtz 1971, 1999). These amazing reedfrogs have an outstanding natural history with annual population cycles and spectacular behavioral (Grafe et al. 2002), morphological and physiological adaptations, and altogether a unique life history strategy to survive the harsh and long dry seasons (Spieler 1997; Linsenmair 1998; Lampert & Linsenmair 2002 and literature cited therein). So far, they are the only tetrapods where sex change has been documented (Grafe & Linsenmair 1989; for literary use of this knowledge see Crichton 1991). To date, Laurent (1951a, 1976, 1983) and Schiøtz (1971) undertook the most detailed morphological approach to disentangle the nomenclatory chaos of these widespread savanna dwelling frogs, which all share a similar morphology (short snout, very large vocal sac in males, transversal gular fold in females, extensive webbing) and call (xylophone like metallic calls; for summary see Schiøtz 1971, 1999).

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However, the mentioned studies of these frogs, using coloration and acoustics, did not provide much insight into their actual taxonomic status (see review by Wieczorek et al. 1998). Only more recently Wieczorek & Channing (1997) and Wieczorek et al. (2000, 2001) started to apply molecular techniques to disentangle the taxonomic chaos. In the course of their work in particular one member of the *H. viridiflavus*-complex/superspecies/species-group, *H. nitidulus* Peters, 1875, was acknowledged species status, a decision previously already applied for mostly pragmatic reasons by e.g. Schiøtz (1967), Drewes (1984) and Rödel (1996, 2000). This widespread West African savanna frog was described by Peters (1875) from "Yoruba (Lagos)", Nigeria. It was treated as a synonym of *H. marmoratus* by Boulenger (1882), as a synonym of *H. picturatus* by Loveridge (1955) and as synonym or subspecies

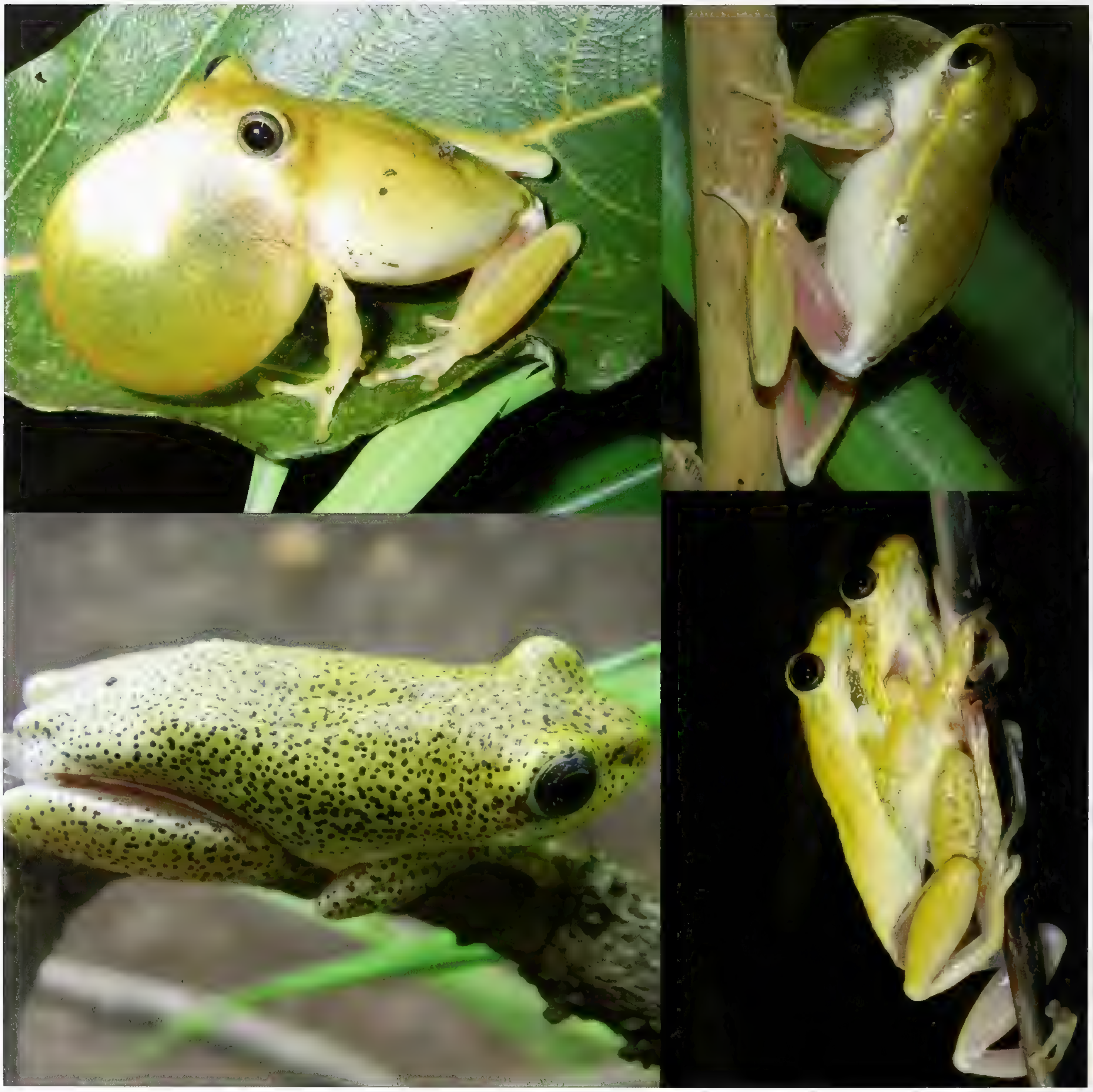

Fig. 1. Life coloration of *Hyperolius spatzi* and *H. nitidulus*; upper left: calling *H. spatzi* male from Sabodala, Senegal, remark uniform yellow color at night; lower left: daytime coloration of *H. spatzi* from Sabodala, Senegal, with numerous minute black points; upper right: calling *H. nitidulus* male from Pendjari National Park, northern Benin, remark dark lateral band; lower right: *H. nitidulus* couple from Lamto reserve, Ivory Coast, remark almost uniform yellow color of male and grey mottling on legs and on the flanks in the female.

Table 1. Morphological differences between *Hyperolius nitidulus* and *H. spatzi* based on data provided in the original descriptions and comments based on type specimens and additional material examined herein. Comments which are already deducible from types only, are given in italic.

Characters	*H. nitidulus*	*H. spatzi*	Comments based on types and additional material
Choanae	large, not hidden beneath edge of mandible	small, hidden below edge of mandible	*similar sized and well visible in both species*
Tongue	large, broad and heart-shaped	unusually small	*tongue in head width spatzi: 3.3 times; nitidulus: 1.7 times*
Snout (dorsal view)	roundish pointed	rounded	truncated in dorsal and lateral view in juveniles, a bit more rounded in adults of both taxa
Snout (lateral view)	flattened or roundish truncate	truncated	truncated in dorsal and lateral view in juveniles, a bit more rounded in adults of both taxa
Position of narins	slightly closer to snout-tip than to eye	in mid distance between eye and snout-tip	*in both species narins closer to snout-tip than to eye*
Position of heals when hind legs arranged to body at right angles	cover or surpass each other	in contact	*surpass each other in both taxa*
Dorsal skin	skin smooth, laterally smooth or with small warts	thick, almost leathery, rough, beset with many small smooth or rough warts	both taxa with rough skinned juveniles in dry season and smooth skinned adults in wet season
Male gular flap	absent	indistinct	present in both taxa
Dorsal color	yellow often with dark spots on back	chalk white or fine speckled with dark-brown	*H. spatzi* with white, brown or yellow back, regularly beset with small black spots; *H. nitidulus* never with such uniform pattern of black spots
Pattern on flanks	dark canthal and lateral stripe (continuous or broken), bordered white dorsally; below the stripe flanks marbled in dark grey and white	No pattern	in *H. spatzi* like on back; *H. nitidulus* with very distinct to rather indistinct black lateral band and dark spots
Body-length	28 mm	21 mm	adults of both species up to about 30 mm

of *Hyperolius viridiflavus* by many other authors (e.g. Laurent 1951a, c, 1961; Schiøtz 1971). The latter author also treated frogs described as *Hyperolius spatzi* Ahl, 1931 from Bakel-Kidira, Senegal (Ahl 1931a, b) as either belonging to *H. nitidulus* (Schiøtz 1967) or as a "subspecies" of *H. viridiflavus* (Schiøtz 1971). In his book, Schiøtz (1999) used the name "spatzi" as a vernacular name, describing "*H. viridiflavus*" populations of uncertain taxonomic status from Senegambia, whereas Rödel (2000) considered *H. spatzi* to represent a junior synonym of *H. nitidulus*. However, already in the late seventies, Böhme (1978) revived the name *H. spatzi* for reedfrogs from Senegal, thus emphasizing their distinctiveness from other West African savanna populations. Recently Emms et al. (2006) adopted this view and reported *H. spatzi* from Gambia. Our recent studies of many *Hyperolius* populations at various West African savanna localities are the basis of a taxonomic reinvestigation of both taxa presented herein.

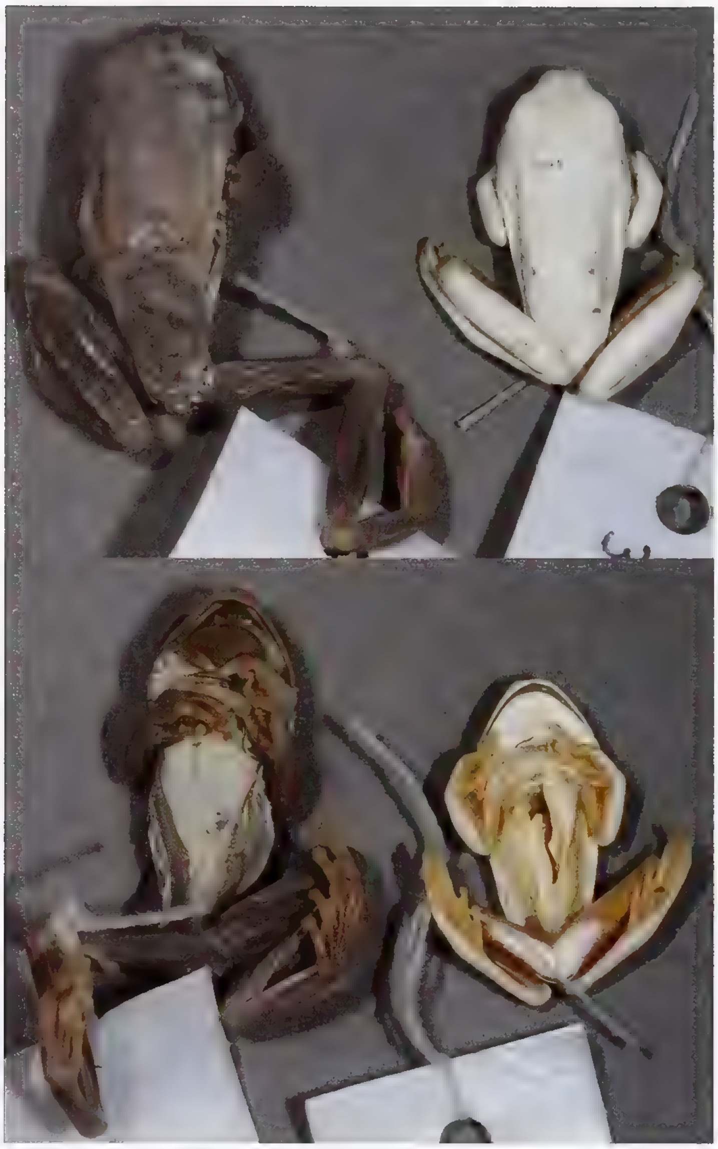

Fig. 2. Dorsal and ventral views of the types of left: *Hyperolius nitidulus* (ZMB 7729, holotype, adult female) and right: *H. spatzi* (ZMB 32602, lectotype, subadult male).

MATERIAL & METHODS

Morphological measurements were taken with a dial caliper (± 0.1 mm) and are given in millimeters. Webbing formulae follow the scheme of Rödel (2000). Museum vouchers originated from the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Museum für Naturkunde Berlin (ZMB; Appendix 2). Calls were recorded with a Sony WM-D6C tape recorder and a directional microphone (Sony ECM-Z157 and Sony ECU-959C9) or an EDIROL R-09 24bit digital recorder (sample rate: 44.1 kHz, record mode: wav_24bit, microphone ECM-950). These calls were analyzed with the program Avisoft SAS Lab Pro 4.5 (R. Specht, Berlin, Germany). For sequence comparisons, we analyzed 247 base pairs (bp) of the mitochondrial 16S ribosomal RNA gene from *Hyperolius spatzi* (ZMB 74280, GenBank HQ113098; Senegal, Sabodala) and *Hyperolius nitidulus* (ZMB 74884, GenBank HQ113099, Sierra Leone, Tingi Hills; no voucher, GenBank HQ113100, Ivory Coast, Mont Sangbé National Park, tissue without voucher). Further hyperoliid gene sequences were obtained from GenBank (Tab. 1). DNA extraction, amplification and sequence alignment followed the procedures as described in Rödel et al. (2009). Uncorrected pairwise sequence divergence was calculated using PAUP*4b10 (Swofford 2002).

RESULTS & DISCUSSION

Morphological comparison. A major problem in using external morphological characters for determination of these frogs is their polymorphism. Schiøtz's (1963, 1967, 1971) described distinct color phases for many *Hyperolius* species, i.e. called F or A and J or B, respectively. The phase F/A of *H. nitidulus/spatzi* refers to the adult/wet season pattern, whereas phase J/B is the juvenile or sub-adult dry season pattern. Young frogs in dry season condition have a rough, warty dorsal skin which is brown below 35°C and chalk white above this temperature (see figs. in Spieler 1997 and Rödel 2000). Adult frogs have smooth skin and a completely different dorsal color pattern (Fig. 1). These morphological differences are part of the amazing aestivation strategy of these frogs (see Linsenmair 1998; Rödel 2000 and literature cited therein).

According to the descriptions by Ahl (1931b) differences between *Hyperolius nitidulus* and *H. spatzi* would be those summarized in Tab. 1 (compare also translations of the original descriptions provided in Appendix 1). Major differences between the descriptions of *H. nitidulus* and *H. spatzi* consist in the fact that the description of the former is based on an adult female, whereas the description of the latter is based on a series of subadult frogs in dry season condition (Fig. 2).

Schiøtz (1967, 1971, 1999) mentioned differences between various West African *H. nitidulus* populations, including a cline in pattern from Sierra Leone (few and small spots on flanks) to Cameroon (broad lateral band; same cline in pattern on the lower legs). He also observed an hour-glass pattern and a dark vocal sac in frogs from Sierra Leone (likewise present in some juveniles in northern Ivory Coast, see Rödel 2000). Our specimens from Sierra Leone neither differed in coloration nor in genetics (see below) from e.g. *H. nitidulus* populations from northern Ivory Coast. Schiøtz (1971) further mentions that frogs from drier northern savannas are more uniform grayish colored, whereas more southern ones, i.e. from the humid savanna types, exhibit a distinct pattern. The latter differences might be related to age. Rödel (2000) reported that older specimens are more distinctly colored. As adult *H. nitidulus* are unable to survive the dry season, all popu-

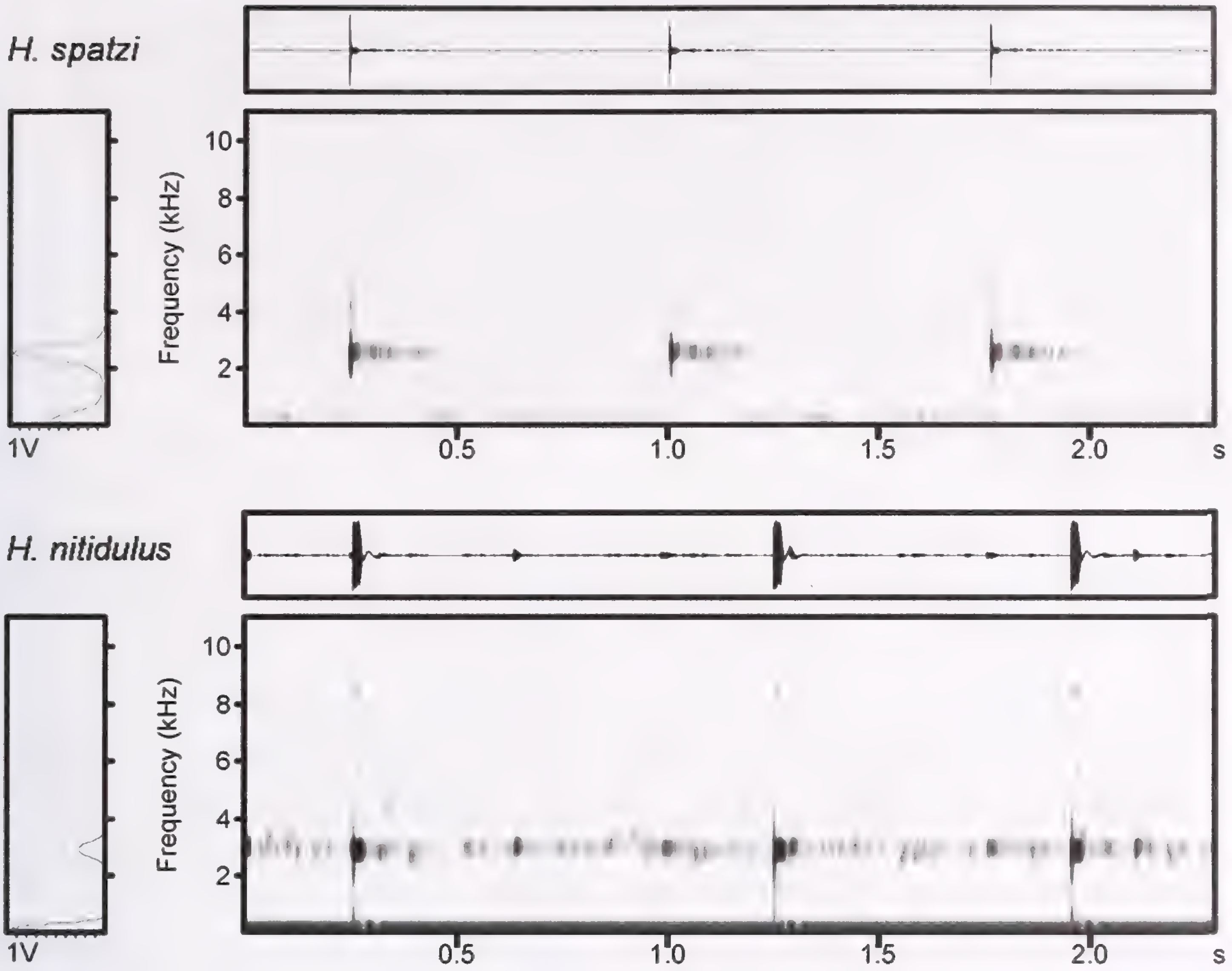

Fig. 3. Waveforms, spectrograms and energy plots of the advertisement calls of *Hyperolius spatzi* (above) and *H. nitidulus* (below; compare Tab. 2). The *Hyperolius spatzi* male from Sabodala, Senegal, was recorded in a terrarium. The *Hyperolius nitidulus* was recorded at a savanna pond in Comoé National Park, Ivory Coast. The background noise is a chorus of other *H. nitidulus* males.

lations are annual (Linsenmair 1998). In more humid savannas, the wet season lasts longer and frogs may reach older ages (and thus potentially a more colorful pattern).

Almost all anatomical differences (position and size of choanae, position of narins, size, shape, length of extremities, head width) deducible from Ahl's (1931a, b) descriptions (compare Tab. 1) are identical among both taxa (for specimens investigated see Appendix 2). Both species have very short, rounded snouts, females posses a typical gular fold and males have very large vocal sacs with a large but diffuse whitish yellow gular flap (gland). Juveniles are often almost indistinguishable. *Hyperolius nitidulus* juveniles show clear dorsolateral bands or an hourglass pattern shortly after metamorphoses (see figs. in Rödel 2000). In dry season conditions they are uniform brown or white. Juvenile *H. spatzi* in dry season conditions are white with many small black dots, the latter sometimes being indistinct. In contrast, adult frogs are distinctively colored. The dorsal surfaces of *H. spatzi* are chalk-white to yellow, densely beset with tiny black spots, whereas *H. nitidulus* is brownish or yellowish with black spots and has black lateral lines and spots (plate 18 in Leaché et al. 2006). *H. nitidulus* has white, yellow or reddish ventral surfaces, whereas these surfaces are exclusively yellow in *H. spatzi* (see fig. 2f in Emms et al. 2006). The hidden parts of legs are pinkish to blood red in both species (Fig. 2 and figs. 430 & 431 in Schiøtz 1999, figs. in Rödel 2000). Generally, females of *H. nitidulus* have a more distinct lateral black pattern than males, which can be almost uniform brown (Fig. 1 and figs. in Rödel 2000). At night, males of both taxa appear uniform yellowish.

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Table 2. Characteristics of the advertisement calls of *Hyperolius spatzi,* recorded in Sabodala, Senegal, and *H. nitidulus,* recorded in the Comoé National Park, Ivory Coast and Mount Nimba, Guinea (Fig. 3). Differences of call length, main frequency and time between calls have been tested by comparing mean values of five males of each species (Wilcoxon test).

		Call length [sec]	Frequency [Hz]	Inter-call intervals [sec]
H. spatzi	mean	0.08	2638.0	1.12
	sd	0.04	139.6	0.80
	N (males)	5	5	5
	N (calls)	25	25	25
H. nitidulus	mean	0.02	2927.6	1.01
	sd	< 0.01	85.1	0.29
	N (males)	5	5	4
	N (calls)	25	25	20
W		616	26	218
P		< 0.0001	< 0.0001	0.4756

Usually, the pattern in *H. nitidulus* remains vaguely visible. The only morphological difference detected by us (herein confirming Ahl 1931a, b), is the size and shape of the tongue. *Hyperolius spatzi* usually have comparatively smaller and narrower tongues than *H. nitidulus*, whose tongue is broad and almost heart-shaped. This is also visible in the type specimens of both species.

Acoustics. The advertisement call of both taxa is a single, pure, metallic and very loud tone (Fig. 3). Choruses of both species resemble xylophones or bells. Although superficially similar, advertisement calls of both taxa showed significant differences. The call of *H. spatzi* was of comparatively longer duration and lower frequency (Tab. 2). The small sample size and the relatively slight differences in call characteristics urge for some caution in their interpretation. However, the acoustic results are not contradicting the specific distinctiveness of *H. nitidulus* and *H. spatzi.*

Genetics. The genetic distances in the investigated fragment of the 16S RNA gene between *Hyperolius spatzi* (N= 1) and *H. nitidulus* (N= 3, originating from Sierra Leone and Ivory Coast) ranged from 5.1–5.6%. The mean distance between *H. spatzi* and various other members of the *H. viridiflavus/marmoratus*-complex (N= 33; including *H. nitidulus*) was 5.9% (± 1.1 SD; range: 3.6–8.7%). The lowest distance was present in comparison to a *H. viridiflavus angolensis*, the highest to a *H. viridiflavus viridiflavus* sample (sequences from GenBank, compare Tab. 3). Mean genetic distances between *H. spatzi* and nine other *Hyperolius* species was 18.7% (± 3.9 sd; range: 11.2–23.2%). The lowest distance present occurred in comparison to *H. fusciventris*, the highest to a *H. cinnamomeoventris* sample (compare Tab. 3).

Based on genetic data (12S and 16S), Wieczorek et al. (2000, 2001) recognized *H. nitidulus* as being distinct on the species level from other members of the *H. viridiflavus* group. Altogether they accepted ten species within this group of which *H. nitidulus* was most distinct (within intraspecific genetic variation 0.7–4.8%; between clade variation 2.4–10.0%; Wieczorek et al. 2001). Our data confirm their results and speak in favor of likewise recognizing *H. spatzi* as a distinct species.

Distribution. *Hyperolius nitidulus* occurs in humid to dry savannas of West Africa (Fig. 4; Lamotte 1966; Schiøtz 1967, 1999; Rödel 2000). Laurent's (1951c) doubts concerning the type locality of *H. nitidulus* were rejected by Schiøtz (1963), by explaining that savanna exists at the type locality, and thus also suitable habitats for *H. nitidulus*. Records have been published for Benin (Nago et al. 2006), Ghana (Schiøtz 1964a, 1967; Hoogmoed 1980; Hughes 1988; Rödel & Agyei 2003; Leaché 2005; Leaché et al. 2006), Burkina Faso (this paper), eastern and central Guinea (Laurent 1951a, c; Schiøtz 1967; Rödel et al. 2004; Hillers et al. 2006, 2008; Greenbaum & Carr 2005), Ivory Coast (Laurent 1951c; Lamotte & Perret 1963; Barbault 1967, 1972; Lamotte 1967; Schiøtz 1967; Vuattoux

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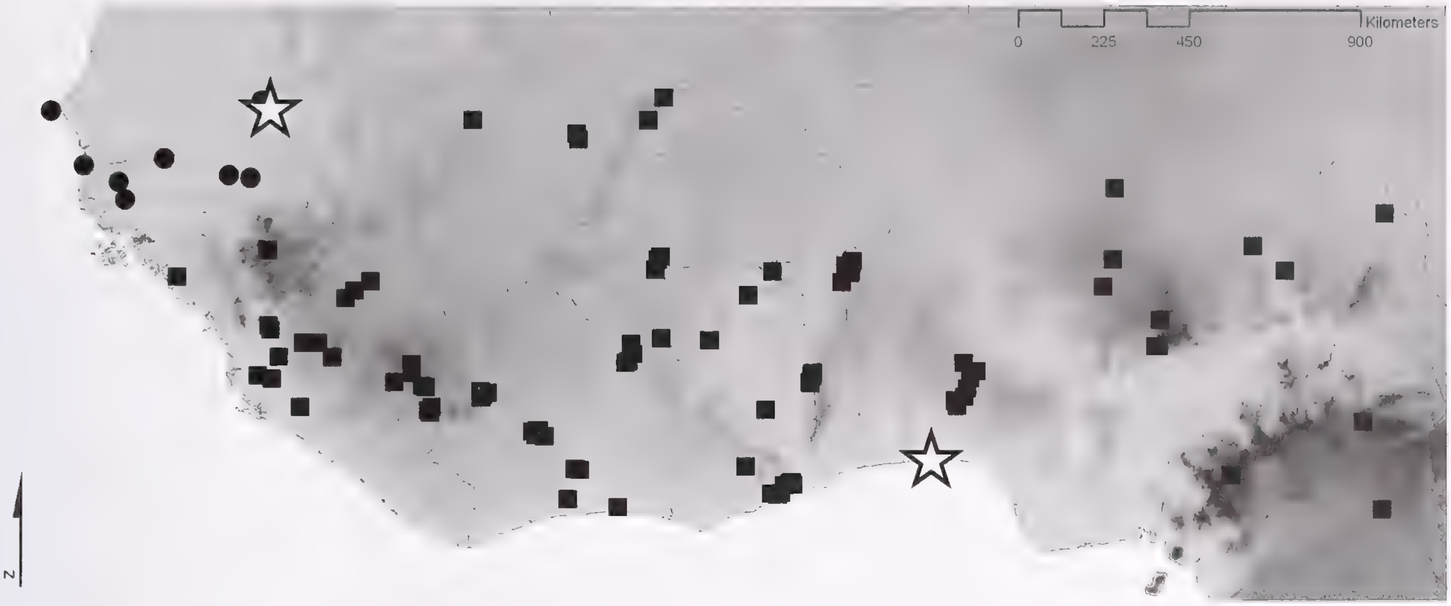

Fig. 4. Known distributions of *Hyperolius spatzi* (circles) and *H. nitidulus* (squares) based on museum and literature records (compare text and Appendix 2); stars indicate positions of type localities of *H. spatzi* (Senegal) and *H. nitidulus* (Nigeria). The north-westernmost record of *H. nitidulus* in Nigeria may refer to *H. pallidus*, southern and central Cameroonian populations are usually referred to two *H. nitidulus* subspecies (compare text and fig. 428 in Schiøtz 1999).

1968; Euzet et al. 1969; Rödel 1996, 1998, 2000, 2003; Spieler 1997; Linsenmair 1998; Rödel & Spieler 2000; Rödel & Ernst 2003; Adeba et al. 2010), Mali (Schiøtz 1967), Nigeria (Schiøtz 1963, 1966, 1967; Walker 1968; Onadeko & Rödel 2009), Sierra Leone (Schiøtz 1964b, 1967; Lamotte 1971), and Togo (Bourgat 1979; Segniagbeto et al. 2007).

Hyperolius spatzi, as defined herein, has been recorded from Senegal (Boettger 1881, as *H. cinctiventris*; Loveridge 1956; Schiøtz 1967; Lamotte 1969; Miles et al. 1978, listed as *H. nitidulus*; Ahl 1931a, b; Böhme 1978), and The Gambia (Andersson 1937 as *H.* sp., but unambiguous description provided; Barnett & Emms 2005 as *H. nitidulus*; Emms et al. 2006). A record from Guinea was actually based on *H. nitidulus* (Hillers et al. 2006; see Appendix 2). Schiøtz (1971) recognized "*H. viridiflavus spatzi*" as a taxonomic unit occurring in Senegambia and provides a map, indicating the distribution of *H. spatzi* and *H. nitidulus*, respectively (fig. 42 in Schiøtz 1971). Padial & de la Riva (2004) believed that *H. nitidulus* and *H. viridiflavus* may occur in southern Mauritania. *Hyperolius viridiflavus* (*sensu stricto*) certainly does not occur in western Africa, including Mauritania. *Hyperolius nitidulus* might reach eastern Mauritania and it seems very likely that *H. spatzi* might be a part of the Mauritanian fauna, as is indicated by the close proximity of the type locality of this species to the boarder of Mauritania (Fig. 4).

Mountains and rivers can act as potential barriers between taxa (e.g. Li et al. 2009, for contrasting results see Gascon et al. 1998). In this case, the Géba and Corubal rivers along the border between Guinea-Bissau and Guinea, might fulfill such a role. It is also possible that the northern foothills of the Fouta Djallon serve as an altitudinal barrier. However, more data from Equatorial Guinea, westernmost Guinea, eastern Senegal, western Mali and Mauritania would be needed to clarify the exact limits of the species' ranges.

The distribution of *H. nitidulus* in Central Africa is more complicated. The species is listed as *H. viridiflavus* (subspecies *H. v. nitidulus, H. v. pallidus*) for Cameroon, the Central African Republic and the Democratic Republic of Congo by Frétey & Blanc (2000). In northern Cameroon and adjacent north-eastern Nigeria, Chad and the Central African Republic (Joger 1990), *H. nitidulus* may be replaced by *H. pallidus* which was described by Mertens (1940) from dry northern Cameroon (Poli near Garua) and which has been treated by Perret (1966) as a full species, and by Schiøtz (1971) and Amiet (1973) as a subspecies of *H. nitidulus*. From Cameroonian savannas, situated a bit further south, two *H. nitidulus* subspecies have been described by Perret (1966). *Hyperolius n. bangwae* occurs in elevated savannas, i.e. Bamenda, Bamiléké, Adamaoua, whereas *H. n. aureus* is said to occur in the drier northern savannas and semi-deserts (Perret 1966; compare e.g. Böhme & Schneider 1987 for some records). This view was adopted by Schiøtz (1971) and Amiet (1973). The latter provided arguments for the treatment of these taxa as subspecies of *H. nitidulus*, i.e. Cameroonian frogs differ from typical *H. nitidulus* by slightly smaller size and slightly duller coloration. The voices are "as good as identical" (Amiet 1973). More recently, Amiet thought that all

Table 3. Genetic distances between *Hyperolius spatzi* (ZMB 74280; GenBank #: HQ113098) and other *Hyperolius* species. Uncorrected p-distances are based on 247 base pairs of mitochondrial 16S ribosomal RNA. Values for *H. nitidulus* are given in bold.

Genus	Species	„Subspecies“	GenBank #	p-distance
Hyperolius	*chlorosteus*		FJ594076	0.214
Hyperolius	*cinnamomeoventris*		FJ594077	0.232
Hyperolius	*concolor*		FJ594078	0.203
Hyperolius	*fusciventris*		FJ594080	0.112
Hyperolius	*guttulatus*		FJ594082	0.133
Hyperolius	*horstocki*		AF282410	0.199
Hyperolius	*kivuensis*		AF282409	0.183
Hyperolius	*naustus*		AF215442	0.219
Hyperolius	*nitidulus*		HQ113099	**0.051**
Hyperolius	*nitidulus*		HQ113100	**0.051**
Hyperolius	*nitidulus*		AF282435	**0.056**
Hyperolius	*picturatus*		FJ594090	0.186
Hyperolius	*viridiflavus*		AF215440	0.056
Hyperolius	*viridiflavus*		AF215441	0.061
Hyperolius	*viridiflavus*		AY323920	0.077
Hyperolius	*viridiflavus*	*angolensis*	AF282411	0.036
Hyperolius	*viridiflavus*	*albofaciatus*	AF282433	0.065
Hyperolius	*viridiflavus*	*aposematicus*	AF282412	0.051
Hyperolius	*viridiflavus*	*argentovittis*	AF282431	0.046
Hyperolius	*viridiflavus*	*bayoni*	AF282413	0.082
Hyperolius	*viridiflavus*	*broadleyi*	AF282414	0.071
Hyperolius	*viridiflavus*	*ferniquei*	AF282416	0.051
Hyperolius	*viridiflavus*	*ferniquei*	AY603987	0.051
Hyperolius	*viridiflavus*	*glandicolor*	AF282417	0.066
Hyperolius	*viridiflavus*	*goetzi*	AF282418	0.066
Hyperolius	*viridiflavus*	*mariae*	AF282419	0.066
Hyperolius	*viridiflavus*	*mariae*	AF282420	0.066
Hyperolius	*viridiflavus*	*marginatus*	AF282430	0.051
Hyperolius	*viridiflavus*	*melanoleucus*	AF282432	0.056
Hyperolius	*viridiflavus*	*pamtherinus*	AF282425	0.051
Hyperolius	*viridiflavus*	*pitmani*	AF282426	0.066
Hyperolius	*viridiflavus*	*marmoratus*	AF282421	0.056
Hyperolius	*viridiflavus*	*ngorongoro*	AF282423	0.066
Hyperolius	*viridiflavus*	*ommatostictus*	AF282424	0.056
Hyperolius	*viridiflavus*	*pyrrhodictyon*	AF282434	0.046
Hyperolius	*viridiflavus*	*rhodesianus*	AF282427	0.038
Hyperolius	*viridiflavus*	*rubripes*	AF282436	0.062
Hyperolius	*viridiflavus*	*swymmertoni*	AF282415	0.071
Hyperolius	*viridiflavus*	*taeniatus*	AF282422	0.056
Hyperolius	*viridiflavus*	*verrucosus*	AF282428	0.062
Hyperolius	*viridiflavus*	*viridiflavus*	AF282429	0.087

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three Cameroonian taxa are subspecies of *H. viridiflavus*, i.e. the highlands of western Cameroon and the Adamaoua plateau being inhabited by *H. v. aureus* (and possibly *H. v. bangwae*), and populations occurring in northern Cameroon (mid-Sudanian, Sudano-Sahelian and Sahelian zones) belong to *H. v. bangwae* and *H. v. pallidus* (J.-L. Amiet pers. comm.).

Conclusions. Our investigations on the type specimens, as well as on additional vouchers, revealed small but distinct morphological (mostly color pattern; tongue shape and size), significant acoustic and large genetic differences (16S gene). Especially the genetic differences are clearly within the range that is thought to be species specific in anurans (Vences et al. 2005a, b; Rödel et al. 2009; Vieites et al. 2009). Our results thus speak in favor of recognizing both taxa as distinct species. A contradicting argument was seen in the very complicated situation of a large variation of color patterns between and within populations of the *Hyperolius viridiflavus/marmoratus* species group(s). Schiøtz (1999) thus questions an approach where the taxonomy for only a small part of the continent would be resolved. However, in West Africa it is possible to assign these frogs to particular names and we thus do not see a reason for avoiding it. We therefore herein resurrect the species status of *H. spatzi*, designate a lectotype from the series of syntypes and redescribe the species based on type and new material.

REDESCRIPTION OF *HYPEROLIUS SPATZI* AHL, 1931.

ZMB 32602 (lectotype; Fig. 2), 74853-74876 (paralectotypes, formerly all ZMB 32602), all from Bakel-Kidira, Senegal, coll. Spatz.

Description of lectotype (all measurements in mm). Subadult frog (male, vocal sac barely developed?); short, compact body; snout-vent length 19.2; head width 7.3, head length 6.9, thus head wider than long; snout short and truncated in dorsal and lateral view; narins angular narrow slit, closer to snout-tip than to eye; tympanum hidden; transversal gular fold; tongue small, narrow, almost parallel and notched anteriorly, tongue width 2.3, tongue length 3.2, tongue 3.3 times in head width; choanae small and round, close to edge of mandible but well visible; dorsal skin slightly granular; belly granular (medially dissected); ventral skin on thighs near vent granular, remaining ventral parts of hind limbs smooth; finger and toe tips enlarged to discs; relative lengths of fingers: 1<2<4<3; basal webbing between fingers; femur length: 8.4; tibia length: 10.4; foot incl. longest toe: 14.0; relative lengths of toes: 1<2<3<5<4; webbing formula: 1 (0), 2 (1.5–0), 3 (1.5–0.5), 4 (1–0), 5 (0); subarticular tubercles on fingers and toes not very prominent. Dorsal surfaces chalk white, densely beset with minute black points; ventral skin on thighs near vent white, remaining parts of thighs and ventral parts of shanks, feet, inner parts of forelimbs, ventral part of hands and fingers fleshy colored.

Variation. Series of paralectotypes almost indistinguishable from lectotype, exclusively subadult frogs in dry season conditions; dorsal skin partly more or less granular than in lectotype; black points on white ground sometimes more distinct or sometimes almost absent. Further material (see Appendix 2) exhibit the following variation: Male snout-vent length: 27.0–31.3 (N= 6); female snout-vent length 30.6 (N= 1); snout shape of adult frogs in dorsal and ventral view slightly more rounded than in juveniles; adults of both sexes in ethanol with dorsal surfaces (incl. upper side of thighs) with brownish ground color (composed of small, very dense brownish points), many very distinct black spots; black spots sometimes a bit more abundant on flanks than on back; some specimens with black spots on throat; others with uniform clear ventral surfaces; tongue in almost all specimens small and comparatively narrow (exception: ZMB 74279). Adult animals in life brownish to yellow with very distinct black spots. These may be not visible during night. Venter yellow.

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APPENDIX 1.

Translations of the original descriptions of *Hyperolius nitidulus* by Peters (1875) and *Hyperolius spatzi* by Ahl (1931a):

Hyperolius nitidulus (Fig. 2): "Body shape equals that of *H. marmoratus*. Snout same length as eye. Tympanum hidden. Belly and ventral surfaces of thighs granular. The outer two fingers and the forth toe, with the exception of the two most distal phalanges, webbed. Dorsally purple grey, shanks likewise colored, whereas the thighs seem to be uncolored. A black band from nose through eye to belly, there band dissolving into black spots on white background; upper lip, flanks below this band, anal region, upper surfaces of forearms, outer and inner edge of shanks and external side of foot to toe tips (in ethanol) white with black spots, which plus/minus fuse. Total length 28 mm; head: 8 mm; head width: 8.5 mm; forearm: 19 mm; hand with 3rd finger: 7 mm; hind leg: 44 mm; foot with fifth toe: 20 mm. From Yoruba (Lagos). [comment added: referring to ZMB 7729, holotype]" Plate 3 (figures 4 and 4a) in Peters (1875) figures the typical wet-season color pattern of this species.

Hyperolius spatzi (Fig. 1): "stocky body shape; vomerine teeth absent; choanae very small, hidden below edge of mandible; tongue unusually small, notched posteriorly; large head, app. 1/3 of body length, wider than long; snout rounded, truncated in lateral view, not or only slightly surpassing mouth, as long as eye, much shorter than distance between anterior corner of eyes, slightly longer than high; *canthus rostralis* rounded but distinct; loreal region vertical, only slightly concave; narines in mid distance between eye and snout-tip; inter-narial distance slightly narrower than inter-orbital distance, the latter twice as wide as upper eyelid; tympanum hidden beneath skin.

Robust fingers, 1/3 to 1/2 webbed; well developed discs; 1st finger shorter than second, second shorter than fourth, which is slightly surpassed by the 3rd finger; 3rd finger as long as snout; subarticular tubercles moderately large, not prominent. Webbing on feet complete with the exception of 4th toe where the last phalanx is without webbing; discs as large as those on fingers; 5th toe slightly longer than 3rd; external metatarsalia tightly fused, tarsal fold absent; very small inner metatarsal tubercle; outer metatarsal tubercle lacking; no tarsal tubercle; subarticular tubercle small, moderately distinct. Tibio-tarsal angle surpasses eye or reaches snout-tip. Femur shorter than tibia, the latter 3.5–4 times longer than wide and twice or slightly less times in body length, longer than foot; heals in contact when hind legs arranged to body at right angles.

Dorsal skin thick, almost leathery, rough, beset with many small smooth or rough warts; ventrum granular; distinct postgular and postpectoral folds; no temporotemporal fold; males with subgular vocal sac and a small, indistinct gular flap.

Coloration in alcohol dorsally chalk white or, rarer, fine speckled with dark-brown. Venter white. Ventral parts of thighs and inner parts of shanks flesh-colored (presumably red in life). No markings at all.

Body length 21 mm. Bakel-Kidira (Upper Senegal region). 26 specimens, Bakel-Kidira, Spatz leg., types [comment added: ZMB 32602, lectotype; 74853-74876, paralectotypes; formerly all ZMB 32602]. The species is named to honor the collector, the well know researcher Spatz, whose collecting activities resulted in a large number of valuable reptiles and amphibians, stored in the Berlin museum."

APPENDIX 2.

Voucher specimens, including types, of *Hyperolius spatzi* and *H. nitidulus* in the ZMB and SMNS collections.

Hyperolius nitidulus**. Benin**: ZMB 74896-74898, Pendjari National Park, Sudan savanna, October 2003, coll. Olaf Grell; ZMB 74890, Pendjari National Park, Tangieta, savanna, N 10°38.317', E 01°15.746', 1 September 2004, coll. G.A. Nago & M.-O. Rödel; **Burkina Faso**: ZMB 74893-74894, Dano, small river in savanna, N 11°14'16.8", W 03°01'24.1", 22 October 2003, coll. T. Moritz; **Ivory Coast**: SMNS 8995.1-2, Ananda, 1993, coll. M.-O. Rödel; SMNS 9680.1-2, Bondoukou, 1996, coll. K. Kouadio; ZMB 74888 & SMNS 8967.1-7, Comoé National Park, savanna, June 1996, coll. M.-O. Rödel; ZMB 74886, Mont Sangbé National Park, Mare Soumarou, island forest in the savanna, pitfall trap, dry season 2001, coll. G. Gbmalin & Y. Cesar; **Guinea**: ZMB 74895, Mont Béro Classified Forest, savanna, N 08°08'30.9", W 08°34'09.6", 1 December 2003, coll. M.A. Bangoura & M.-O. Rödel; ZMB 74891-74892 Nimba Mountains, savanna Séringbara, with big ponds, close to village, N 07°36.181', W 08°29.769', 18 May 2006, coll. T.N.-S. Loua & A. Hillers; ZMB 74889, Pic de Fon/Simandou range, Banko, savanna, 11 July 2004, coll. M.A. Bangoura & K. Kamara; ZMB 74882, Boké Préfécture/Kolaboui, swampy area in secondary forest island, N 10°45.075', W 14°27.040', 23 & 24 April 2005, coll. M.A. Bangoura & A. Hillers (originally listed as *H. spatzi* in Hillers et al. 2006); **Nigeria**: ZMB 7729 (holotype), Yoruba (Lagos), coll. Krause; **Sierra Leone**: ZMB 74884-74885, Tingi Hills, big pond with a few trees around and swampy area in savanna, N 08º51.047', W 10º46.502', 427 m a.s.l., 5 June 2007, coll. J. Johnny & A. Hillers; **Togo**: ZMB 39028, station Sokode, coll. Schröder.

Hyperolius spatzi**. Gambia**: ZMB 74877, Abuko Nature Reserve, savanna, 2005, coll. L. Barnett & C. Emms; **Senegal:** ZMB 32602 (lectotype), 74853-74876 (paralectotypes, formerly all ZMB 32602), Bakel-Kidira, coll. Spatz; ZMB 74279, Sabodala, ponds and puddles in degraded farmbush savanna next to Oromin camp, N 13°09.368', W 12°06.882', 12 September 2009, coll. A. Hillers & Y. Mané; ZMB 74280-74285, Sabodala, in and around big pond in farmbush savanna/grassland, with some rocks, N 13°07.259', W 12°07.622', 7 September 2009, coll. A. Hillers & Y. Mané.

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Genetic variability in mainland and insular populations of *Podarcis muralis* (Reptilia: Lacertidae)

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Abstract. Allozyme electrophoresis was used to study the distribution of genetic variation within and among mainland and insular populations of the lacertid lizard *Podarcis muralis* from western, southern and eastern Europe. Genetic variability in the species is low and genetic subdivision is high. The highest values of percent polymorphism and heterozygosity were found in the samples from two Tyrrhenian islands (Elba Island, La Scola Islet). The occurrence of higher levels of genetic variability in insular populations is probably because these populations inhabit marginal environments characterized by temporal-ecological instability. In these environments high heterozygosity levels can be preserved after colonization events, unless founder populations are so small that bottleneck effects occur. The genetic heterogeneity analysis demonstrates a certain amount of genetic differentiation among local populations of *P. muralis*, with a relatively high level of genetic subdivision. Allozyme data show that genetic variation in *P. muralis* is distributed into two major population groups: the first includes the closely related samples from Spain and SW France, the second the genetically recognizable samples from Germany, Italy, and Greece. The average genetic distance between the two groups is relatively high (Nei's $D = 0.059$), with D ranging from 0.043 to 0.100.

Key words. *Podarcis muralis*, Lacertidae, allozyme electrophoresis, population heterogeneity, Tyrrhenian islands, Europe.

INTRODUCTION

There have been numerous surveys of the genetic structure of insular populations of vertebrates, especially reptiles (e.g. Soulé & Yang 1974; Gorman et al. 1975; Patton et al. 1975). From these studies it became evident that many demographic, historical, and geographic factors influence the pattern of genetic variation in the insular populations (e.g. Soulé et al. 1973; Soulé 1976).

The Mediterranean lacertid lizards of the genus *Podarcis* seem to be particularly useful for this type of investigation because they are widespread on several Mediterranean islands and are normally characterized by high inter- and intra-population morphological and genetic variability (e.g. Harris & Arnold 1999; Arnold & Ovenden 2002; Corti & Lo Cascio 2002; Salvi et al. 2009). Although the evolutionary significance of the pattern of variation observed in these lacertid lizards has been unstudied for most taxa, in some cases at least it was pointed out that species which are characterized by a high degree of phenotypic plasticity in the pattern of the upper parts may have levels of genetic variability higher than those found in the morphologically low variable species (see e.g. Selander 1976; Capula 1994a, 1996, 1997; Losos et al. 1997; Capula & Ceccarelli 2003; Caputo et al. 2008).

In this paper, based primarily on allozyme data, the distribution of genetic variation within and among mainland and insular populations of the lacertid lizard *Podarcis muralis* from western, southern and eastern parts of its European range was estimated. *Podarcis muralis* was chosen as it is a morphologically and ecologically variable species occurring in a wide variety of habitats over its distribution range, which extends from the northern border of the Iberian Peninsula to north-western Turkey, and throughout central and southern Europe (Arnold & Ovenden 2002; Corti & Lo Cascio 2002). In the northern part of its range this lizard is typically a thermophilous and lowland species, with a reduced variability in the pattern of the upper parts, while in the southern part it is more often a mountain species, occurs especially in wet and shady habitats, and is characterized here by high phenotypic variability (see Capula et al. 1993, 2009; Corti et al.

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Table 1. Geographic and collecting data for the *Podarcis muralis* samples used in this study.

Population	Locality	Sample size
A	Guadarrama (Spain)	5
B	Anso (Spain)	5
C	Ordesa (Spain)	3
D	Deba (Spain)	4
E	Albaran (Spain)	3
F	Bidache (SW France)	5
G	Le Chiroulet (SW France)	5
H	St. Gaudens (SW France)	5
I	Bonn (Germany)	5
J	Cavalese (Italy)	20
K	Cesena (Italy)	20
L	Resceto (Italy)	2
M	Chiusdino (Italy)	6
N	Populonia (Italy)	4
O	Uccellina Mountains (Italy)	3
P	Ostia (Italy)	10
Q	Elba Island, Tuscan Archipelago (Italy)	10
R	Scoglietto di Portoferraio Islet, Tuscan Archipelago (Italy)	2
S	Gorgona Island, Tuscan Archipelago (Italy)	4
T	Pianosa Island, Tuscan Archipelago (Italy)	2
U	La Scola Islet, Tuscan Archipelago (Italy)	2
V	Palmaiola Island, Tuscan Archipelago (Italy)	3
Z	Viotia (Greece)	6

in press). Allozyme variation in some Italian, Spanish and Austrian populations of *P. muralis* was studied by Capula (1997), who provided evidence of high level of genetic variability in insular populations. Genetic variation and differentiation in the Italian populations of the species were recently investigated also by Caputo et al. (2008) and Giovannotti et al. (2010), based on the sequencing of a portion of a mitochondrial gene.

MATERIAL AND METHODS

Sampling. Samples of *P. muralis* used in this study were obtained from 17 mainland localities of western, southern and eastern Europe (Spain, SW France, Germany, Italy, Greece) and six islands of the Tuscan Archipelago in the Tyrrhenian Sea (Elba, Scoglietto di Portoferraio, Gorgona, Pianosa, La Scola, Palmaiola). The precise geographic origin of each sample and the number of individuals analysed per population are indicated in Table 1.

Electrophoresis. The electrophoretic analysis was undertaken for 134 specimens from all 23 localities. Standard horizontal starch gel electrophoresis was performed on tail muscle tissue, parts of which were crushed in 0.1 mL of distilled water. Gene products for the following 21 presumptive enzyme loci were analysed: glycerol-3-phosphate dehydrogenase (E.C. 1.1.1.8, ∝*Gpd*), lactate dehydrogenase (E.C. 1.1.1.27, *Ldh-1*, *Ldh-2*), malate dehydrogenase (E.C. 1.1.1.37, *Mdh-1, Mdh-2*), malic enzyme (E.C. 1.1.1.40, *Me-1, Me-2*), isocitrate dehydrogenase (E.C. 1.1.1.42, *Idh-1, Idh-2*), 6-phosphogluconate dehydrogenase (E.C. 1.1.1.44, *6Pgd*), glyceraldehyde-3-phosphate dehydrogenase (E.C. 1.2.1.12, *Gapd*), superoxide dismutase (E.C. 1.15.1.1, *Sod-1*), glutamate-oxaloacetate transaminase (E.C. 2.6.1.1, *Got-1, Got-2*), creatine kinase (E.C. 2.7.3.2, *Ck*), adenosine deaminase (E.C. 3.5.4.4, *Ada*), carbonic anhydrase (E.C. 4.2.1.1, *Ca*), mannose-6-phosphate isomerase (E.C. 5.3.1.8, *Mpi*), glucose-6-phosphate isomerase (E.C. 5.3.1.9, *Gpi*), phosphoglucomutase (E.C. 5.4.2.2, *Pgm-1, Pgm-2*) (enzymes codes are accord-

Table 2. Chi-square values resulting from contingency χ^2 analysis of the polymorphic loci among populations of *Podarcis muralis*. d.f. = degree of freedom; NS = nonsignificant.

Locus	**No. of alleles**	χ^2	**d.f.**	**P**
Ldh-1	2	172.417	22	<0.001
Ldh-2	2	33.841	22	<0.05
Me-1	4	462.317	66	<0.001
Me-2	2	32.622	22	NS
6Pgd	4	222.142	66	<0.001
Gapd	2	42.987	22	<0.004
Got-1	2	63.179	22	<0.001
Pgm-2	2	80.490	22	<0.001
Ca	2	75.142	22	<0.001
Gp-1	2	24.986	22	NS
Gp-2	2	38.449	22	NS
Gp-3	3	331.439	44	<0.001
Total		**1580.010**	**374**	**<0.001**

ing to Richardson et al., 1986). In addition, three unidentified non-enzymatic proteins were studied: *Gp-1, Gp-2, Gp-3*. The buffer systems used, electrophoretic procedures, staining techniques, and loci and allele designations were those described by Capula (1990, 1994b).

Analysis. Genotypic and allelic frequencies were determined by direct counts from allozyme phenotypes, and the resulting data were analysed by various statistical methods to describe the genetic structure of the *P. muralis* populations. Genotypic proportions expected on the basis of Hardy-Weinberg equilibrium were calculated by Levene's formula (Levene 1949) for small samples. The statistical significance of departures from Hardy-Weinberg equilibrium was estimated using a test for calculating exact significance probabilities, analogous to Fisher's exact test (Elston & Forthofer 1977). To determine whether the heterogeneity in the genotypic distribution reflects differences in allele frequencies, the variation in genic proportions among populations was subjected to a contingency χ^2

Table 3. Genetic variability parameters in *Podarcis muralis* populations. *A*, mean number of alleles per locus; *P*, mean proportion of polymorphic loci; H_o, observed mean heterozygosity; H_e, expected mean heterozygosity; SE, standard error.

Population	*A*	*P*	H_o	**SE**	H_e	**SE**
Guadarrama	1,0	0.0	0.000	0.000	0.000	0.000
Anso	1.0	0.0	0.000	0.000	0.000	0.000
Ordesa	1.0	4.2	0.026	0.026	0.022	0.022
Deba	1.0	4.2	0.010	0.010	0.010	0.010
Albaran	1.0	0.0	0.000	0.000	0.000	0.000
Bidache	1.1	8.3	0.038	0.027	0.038	0.027
Le Chiroulet	1.0	4.2	0.008	0.008	0.008	0.008
St. Gaudens	1.1	4.2	0.031	0.031	0.029	0.029
Bonn	1.0	4.2	0.015	0.015	0.015	0.015
Cavalese	1.0	0.0	0.000	0.000	0.000	0.000
Cesena	1.1	12.5	0.038	0.023	0.040	0.024
Resceto	1.1	8.3	0.038	0.027	0.042	0.029
Chiusdino	1.2	16.7	0.064	0.032	0.066	0.033
Populonia	1.1	8.3	0.038	0.027	0.036	0.025
Uccellina Mountains	1.2	12.5	0.038	0.028	0.067	0.039
Ostia	1.1	12.5	0.031	0.018	0.030	0.017
Elba Island	1.1	12.5	0.077	0.046	0.055	0.031
S.to Portoferraio Islet	1.1	12.5	0.019	0.019	0.077	0.043
Gorgona Island	1.1	8.3	0.029	0.021	0.028	0.020
Pianosa Island	1.1	8.3	0.038	0.027	0.042	0.029
La Scola Islet	1.2	16.7	0.077	0.046	0.097	0.046
Palmaiola Island	1.1	8.3	0.032	0.023	0.024	0.017
Viotia	1.0	0.0	0.000	0.000	0.000	0.000

Table 4. Values of Nei's (1978) unbiased genetic distance among populations of *Podarcis muralis*. For geographical origin of populations (A–Z) see Table 1.

	POPULATION																					
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	Z
A	–																						
B	0.000	–																					
C	0.003	0.003	–																				
D	0.000	0.000	0.003	–																			
E	0.000	0.000	0.003	0.000	–																		
F	0.010	0.010	0.000	0.008	0.010	–																	
G	0.000	0.000	0.003	0.000	0.000	0.009	–																
H	0.006	0.006	0.000	0.007	0.006	0.000	0.007	–															
I	0.070	0.070	0.074	0.071	0.070	0.083	0.071	0.079	–														
J	0.043	0.043	0.046	0.043	0.043	0.054	0.043	0.050	0.026	–													
K	0.055	0.055	0.059	0.056	0.055	0.068	0.056	0.063	0.039	0.011	–												
L	0.043	0.043	0.043	0.044	0.043	0.050	0.044	0.046	0.027	0.000	0.001	–											
M	0.046	0.046	0.049	0.046	0.046	0.058	0.046	0.054	0.013	0.009	0.014	0.006	–										
N	0.046	0.046	0.050	0.047	0.046	0.059	0.047	0.054	0.013	0.003	0.004	0.000	0.001	–									
O	0.053	0.053	0.057	0.053	0.053	0.065	0.053	0.061	0.006	0.008	0.004	0.001	0.000	0.000	–								
P	0.045	0.045	0.049	0.045	0.045	0.057	0.045	0.053	0.022	0.002	0.005	0.000	0.005	0.000	0.001	–							
Q	0.059	0.059	0.063	0.059	0.059	0.072	0.059	0.067	0.042	0.014	0.010	0.010	0.021	0.013	0.009	0.012	–						
R	0.082	0.082	0.087	0.083	0.082	0.096	0.082	0.091	0.029	0.036	0.047	0.037	0.017	0.029	0.017	0.034	0.042	–					
S	0.045	0.045	0.048	0.045	0.045	0.057	0.045	0.052	0.011	0.001	0.013	0.002	0.003	0.000	0.001	0.001	0.016	0.027	–				
T	0.043	0.043	0.047	0.044	0.043	0.056	0.044	0.051	0.027	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.032	0.002	–			
U	0.082	0.082	0.087	0.083	0.082	0.097	0.083	0.092	0.047	0.036	0.041	0.038	0.029	0.035	0.024	0.037	0.031	0.000	0.033	0.026	–		
V	0.045	0.045	0.049	0.046	0.045	0.057	0.045	0.053	0.023	0.002	0.012	0.002	0.003	0.003	0.002	0.003	0.010	0.020	0.002	0.000	0.020	–	
Z	0.087	0.087	0.091	0.087	0.087	0.100	0.087	0.095	0.035	0.043	0.055	0.043	0.031	0.035	0.030	0.041	0.059	0.014	0.034	0.043	0.059	0.038	–

analysis (Workman & Niswander 1970). The genetic variability of populations was estimated using the following parameters: mean number of alleles per locus (*A*); percentage of polymorphic loci, at the 99% level (*P*); observed mean heterozygosity (H_o); expected mean heterozygosity in Hardy-Weinberg equilibrium (H_e) (unbiased estimate; Nei 1978). The genetic relationships among the studied populations were evaluated using Nei's unbiased genetic distance (*D*, Nei 1978). All genetic variability and genetic distance measures were calculated using the computer program BIOSYS-2 (Swofford & Selander 1999). An estimation of phenetic relationships among populations was obtained by generating a phenogram of all samples by means of the unweighted pair-group method with arithmetic averaging (UPGMA) based on the matrix of Nei's unbiased genetic distances (Sneath & Sokal 1973).

RESULTS

Of the 24 electrophoretic loci analysed, ten (46%) were monomorphic and fixed for the same allele in all samples (*Mdh-1, Mdh-2, Idh-2, Gapd, Sod-l, Got-2, Mpi, Gpi, Pgm-1, Ada*). Fourteen loci (54%) were found to be polymorphic (*∝Gpd, Ldh-l, Ldh-2, Me-l, Me-2, Idh-l, 6Pgd, Got-l, Ck, Pgm-2, Ca, Gp-1, Gp-2, Gp-3*). The *Me-1* and *Pgm-2* loci only were highly polymorphic, while the other 12 loci were weakly polymorphic. Four samples out of the 23 analysed were characterized by a unique allele (sensu Slatkin 1987): St. Gaudens ($6Pgd^{110}$), Ostia ($Gp\text{-}1^{105}$), Gorgona Island ($Me\text{-}2^{105}$), Elba Island ($Got\text{-}1^{104}$). The results of the contingency χ^2 analysis are given in Table 2. The analysis reveals that 9 out of 12 variable loci exhibit statistically significant heterogeneity in the allele frequencies. This result shows that there are significant differences among the gene pools of the studied samples, indicating local genetic differentiation and a relatively high degree of substructuring among populations. Significant deviations from Hardy-Weinberg equilibrium in the direction of heterozygote deficiences were found in the following populations and loci: Bonn (*Me-l*, $P<0.005$), Chiusdino (*Gp-3*, $P<0.05$).

Genetic variability parameters (*A, P,* H_o, H_e) are reported in Table 3. The overall number of alleles per locus (*A*) was 1.07, ranging from 1.0 to 1.2. The proportion of polymorphic loci (*P*) ranged from 0 (Guadarrama, Anso, Albaran, Cavalese, Viotia) to 16.7% (Chiusdino, La Scola Islet), averaging 7.25%. The observed heterozygosity (H_o) showed a similar trend, ranging from 0 (Guadarrama, Anso, Albaran, Cavalese, Viotia) to 0.077 (Elba Islands, La Scola Islet), and averaging 0.028. The samples from Spain, Germany and Greece are characterized by very low levels of genetic variability (Spain: average $P = 1.68\%$, average $H_o = 0.007$; Germany: $P = 3.8\%$, $H_o = 0.015$; Greece: $P = 0\%$, $H_o = 0$) when compared with the ones from France (average $P = 5.57\%$, average $H_o = 0.023$) and mainland Italy (average P=10.11%, average $H_o = 0.036$). However, it must be noted that Germany and Greece were represented in the analysis only by a sample respectively. Percent polymorphism and observed heterozygosity detected in island populations from the Tuscan Archipelago (Tyrrhenian Sea) were higher than those found in mainland samples (islands: average $P = 9.52\%$; average H_o= 0.045; mainland: average $P = 5.89\%$; average H_o= 0.022); however the differences in polymorphism and heterozygosity values between mainland and insular samples were not statistically significant (*P*, P = 0.141; H_o, P = 0.029, t-test). The samples from La Scola and Elba islands show the highest heterozygosity ($H_o = 0.077$), and the sample from La Scola Islet exhibits the greatest genetic variation, with $A = 1.2$, $P = 16.7\%$, and $H_o = 0.077$.

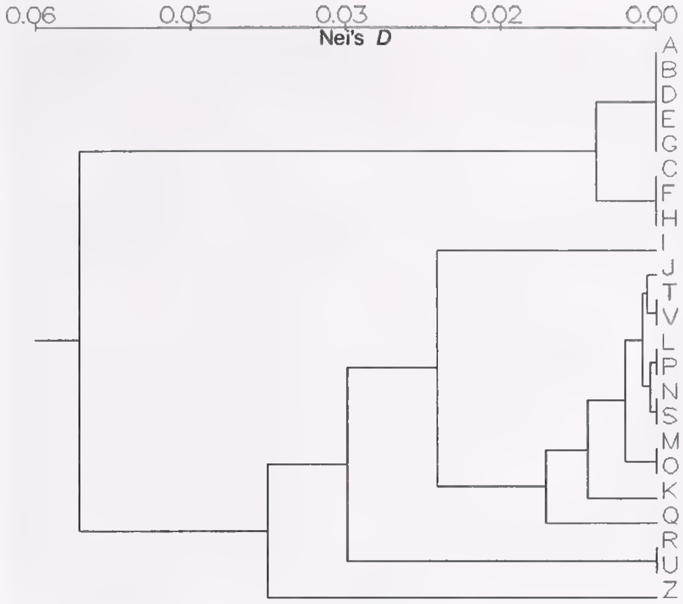

Fig. 1. Phenogram generated by UPGMA cluster analysis based on Nei's (1978) unbiased genetic distances among *Podarcis muralis* populations. For geographic origin of populations (A–Z) see Table 1.

The values of genetic distance for each pairwise comparison are given in Table 4. Nei's genetic distance (*D*) ranges from 0 to 0.100, averaging 0.036. Based on the analysis of genetic distance data, two main population groups can be recognized: the first includes the samples from Spain and SW France, which are genetically very close (average $D = 0.003$; *D* ranging from 0 to 0.010), the second includes all other samples (Germany, Italy, Greece) (average $D = 0.017$; *D* ranging from 0 to 0.059; see Table 4). The ave-rage genetic distance between the two groups is relatively high ($D = 0.059$; *D* ranging from 0.043 to 0.100). The comparison between the populations from western Europe (Spain, SW France) and Greece (Viotia) gives the highest genetic distances (*D* ranging from 0.087

to 0.100; see Table 4). Genetic differentiation was rather low among insular populations from the Tuscan Archipelago (average $D = 0.017$; D ranging from 0 to 0.042), and relatively low between insular and mainland populations (average $D = 0.040$).

The genetic relationships among the samples studied are presented in Figure 1. The UPGMA clustering procedure revealed two main clusters in the phenogram constructed on the basis of the matrix of Nei's unbiased genetic distances. The first cluster includes the closely related samples from Spain and SW France. Within the second cluster the existence of four subclusters should be noted. The first subcluster includes the sample from Bonn (Germany), which is linked to the subcluster containing the closely grouped samples from Italy and four Tyrrhenian islands (Elba, Palmaiola, Pianosa, Gorgona), the third includes the samples from other two Tyrrhenian islands, i.e. Scoglietto di Portoferraio and La Scola, the fourth contains the sample from Viotia (Greece).

DISCUSSION

The results of the allozyme analyses indicate that genetic variability is relatively low in *P. muralis*. The Common wall lizard shows values of polymorphism and heterozygosity higher than those estimated by Capula (2004) for *P. raffonei* ($P = 4.8\%$; $H_o = 0.011$), similar to those observed by Capula & Ceccarelli (2003) for Italian populations of *P. sicula* ($P = 10\%$; $H_o = 0.029$), and lower than (i) those detected in the phylogenetically related *P. wagleriana* from Sicily ($P = 15\%$; $H_o = 0.037$; Capula, 1994b) and *P. tiliguerta* from Sardinia and Corsica ($P = 22\%$; $H_O = 0.066$; Capula, 1996), (ii) the average ones calculated by Capula (1990) for nine species of the genus *Podarcis* ($P = 13\%$; $H_o = 0.053$), and (iii) the average ones calculated by Nevo (1978) for 17 species of reptiles ($P = 22\%$; $H_o = 0.047$). The highest values of heterozygosity were found in the samples from Elba Island and La Scola Islet (Tuscan Archipleago, Tyrrhenian Sea), whereas the lowest ones were observed in some samples from Spain (Guadarrama, Anso, Albaran), Italy (Cavalese) and Greece (Viotia). Based on the theory (see e.g. Nei et al. 1975, Gorman et al. 1975, 1978) we expected to find low levels of genetic variability in the insular samples of *P. muralis*. Our results were in some way not congruent with these expectations, as some samples from the Tuscan Archipelago (e.g. Elba, La Scola) were characterized by levels of percent polymorphism and heterozygosity higher than those found in most of the populations from mainland Italy, Spain, SW France, Germany and Greece. This result in agreement with the allozyme data provided by Capula (1997) indicating that the insular *P. muralis* populations from Elba Island, Isolotto di Porto Ercole Islet and Argentarola Islet (Tyrrhenian islands) are characterized by levels of percent polymorphism and heterozygosity higher than those found in the populations from the Italian Peninsula, and much higher than those observed in the continental populations from the Italian Alps, Spain and Austria (Capula 1997). Within the lacertid lizards, levels of genetic variation are known to be large only in mainland populations of a few species (e.g. Adriatic populations of *P. sicula*: average $H_o = 0.09$ (Gorman et al. 1975); *Acanthodactylus* spp.: average $H_o = 0.18$, average $P = 50\%$; Blanc & Cariou 1980), while populations living on relict islands and on tiny fringing islands (i.e. very small islands that are separated by a short linear distance from the mother island or continent) are usually characterized by very low values of per cent polymorphism and heterozygosity (Gorman et al. 1975). However, the investigated Tyrrhenian islands can be considered as relict islands, as their lizard populations are genetically differentiated from the mainland ones. Moreover, one of the islands considered here (Elba) is a large island (223 km^2), while the other (La Scola) is a tiny island (0.016 km^2), and both are separated by a relatively short geographic distance from mainland (peninsular Italy).

Among reptiles, high levels of genetic variation found in populations of some species (e.g. *Podarcis sicula*, *Cnemidophorus tigris*) are ascribed to high vagility and consequent low levels of inbreeding (Gorman et al. 1977). This does not seem to be true in the genetically highly variable species of *Acanthodactylus*, as these are territorial lizards (Blanc & Cariou 1980). *Podarcis muralis* is a territorial lizard as well (Steward 1965), but in this case only some populations – almost exclusively island populations (Elba and La Scola: this paper; Elba, Isolotto di Porto Ercole, Argentarola: Capula 1997) – exhibit high genetic variability. As suggested by Capula (1997), this is probably because the insular populations inhabit marginal environments characterized by temporal and ecological instability. According to Lewontin (1974), in such environments no particular genotype is favoured for long periods and natural populations usually show levels of genetic variability higher than those found in more stable environments. On the basis of these considerations, finding greater genetic variability in insular populations of *P. muralis* could indicate that high heterozygosity levels can be preserved after colonization events in marginal populations of vertebrates, unless founder populations are so small that bottleneck effects occur.

The genetic heterogeneity analysis demonstrates a certain amount of genetic differentiation among local populations of *P. muralis*, with a relatively high level of genetic subdivision. Allozyme data show that, at the scale of the study, genetic variation in *P. muralis* is distributed into two major population groups: the first includes the closely related samples from Spain and SW France, the second the genetically recognizable samples from Germany, Italy, and Greece. Genetic distance values found between the two groups are relatively high (Nei's *D* ranging from 0.043 to 0.100), although falling below those normally encountered comparing populations of well recognized biological species of the genus *Podarcis* (see e.g. Mayer 1981; Thorpe 1983; Capula 1994a, b, c, 1996). The high genetic affinity between the French and Spanish samples is congruent with their geographic origin, as French samples are from Pyrenean localities (F–H) close to the Spanish ones (A–E). On the other hand, the large geographic distances separating the French localities from the German one (Bonn) could explain the relatively high genetic differentiation observed between the samples from these countries, which cluster separately in the UPGMA phenogram (see Fig. 1).

The data presented here are in agreement with the results of the allozyme investigations carried out by Capula (1997) on some *P. muralis* populations from Italy, Spain and Austria, and are congruent with the results of the molecular investigations (analysis of mitochondrial DNA sequences) carried out by Caputo et al. (2008) and Giovannotti et al. (2010) on several Italian samples, which indicate a certain amount of molecular divergence among *P. muralis* populations, and a pronounced geographical structure of the Italian populations.

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Intraspecific variability of the Carpetane Lizard (*Iberolacerta cyreni* [Müller & Hellmich, 1937]) (Squamata: Lacertidae), with special reference to the unstudied peripheral populations from the Sierras de Avila (Paramera, Serrota and Villafranca)

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Abstract. Canonical Discriminant (CDA), ANOVA and ANOSIM analyses were calculated for all recently known distribution areas of *Iberolacerta cyreni* including several small and unstudied peripheral populations. The only differentiated sample is Guadarrama (the nominate subspecies), with very limited overlap in the CDA (correct classification > 70%) and different from nearly all the other samples in ANOSIM. Guadarrama is a recently differentiated but well diagnosable (morpho)subspecies (with lower values of dorsalia, ventralia and greater values of circumanalia). Despite the mtDNA differences of the Béjar specimens, their morphology is largely equivalent to that of *I. cyreni castiliana* (Gredos), but clearly differ in their female body elongation (near 1 cm) with shorter limbs, a possible strategy to increase clutch size. Populations from the Sierras de Avila (Villafranca, Serrota and Paramera) are very similar among them. Villafranca (in males) together with Béjar (in females) are the most connected samples in MST, and the root of the species differentiation from a morphological point of view, once discarded geographical and climatic influence on morphology. All populations except Guadarrama shall be considered as *I. c. castiliana* by their morphological identity with Gredos. These morphological similarities probably are the reflect of extensive gene flow among them, responsible of maintaining their morphology largely equivalent.

Key words. Lacertidae, *Iberolacerta cyreni*, Intraspecific variability, subspecies, Geographical variation, Iberian Peninsula.

Resumen. Se ha calculado un Análisis Discriminante Canónico, ANOVA y ANOSIM con toda el área de distribución de *Iberolacerta cyreni,* incluyendo varias poblaciones periféricas no estudiadas hasta la fecha. La única muestra diferenciada es Guadarrama (la subespecie nominal), con muy poco solapamiento en el CDA (clasificación correcta > 70%) que difiere de prácticamente todas las demás muestras en el ANOSIM. Guadarrama es una población recientemente diferenciada, pero bien diagnosticable como (morfo)subespecie (valores bajos de dorsalia y ventralia, y altos de circumanalia). A pesar de las diferencias mitocondriales de Béjar, su morfología es ampliamente asimilable a *I. c. castiliana* (Gredos), siendo destacable el relativo elongamiento corporal de las hembras (casi 1 cm) con miembros proporcionalmente cortos, una posible estrategia para incrementar el tamaño de puesta. Las poblaciones de las Sierras de Ávila (Villafranca, Serrota y Paramera) son muy similares entre sí. Villafranca junto con Béjar (en machos y hembras respectivamente) están morfológicamente en la raíz de la diferenciación de la especie (MST), una vez descartada cualquier influencia climática o de distancia geográfica. Excepto Guadarrama, todas deben considerarse como *I. c. castiliana* por su identidad morfológica con Gredos, lo que refleja la probable presencia de un flujo genético extensivo y reciente entre ellas.

INTRODUCTION

The Spanish Sistema Central consists of a series of Sierras, more or less aligned in a ENE-WSW direction, which separate the Duero (to the North) and Tajo (to the South) river drainages, or what is the same, the Old and New Castile plateauxes. It runs from the Portuguese Serra da Estrela (inhabited by a relict population of *Iberolacerta monticola* [Boulenger, 1905]), across the Spanish Sierra de Gata (apparently too low and dry for *Iberolacerta*), the Sierra de Francia with *Iberolacerta martinezricai* (Arribas, 1996) and the main part of the Spanish portion of its range (over 240 km in length), which is inhabited in several points by populations of the Carpetane Lizard (*Iberolacerta cyreni* [Müller & Hellmich, 1937]).

The Carpetane Lizard is widespread through the main parts of the Sistema Central and is mainly known from Sierras de Béjar, Gredos and Guadarrama (Fig. 1). It was raised to species level (Arribas 1996) based on allozymes (Mayer & Arribas 1996), karyology (heterochromatinization of sex-chromosome and localization of the NORs;

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Odierna et al. 1996) and adult and hatchlings pattern and coloration. Two subspecies were defined, the nominal *I. c. cyreni* from Guadarrama (type locality: Puerto de Navacerrada), and *I. cyreni castiliana* from Gredos (type locality: Circo de Gredos, Avila) to which frequently are assimilated Béjar specimens. This latter subspecies differs from the nominate one by a reduced dark pattern, more dorsalia, ventralia, slightly larger diameter of the masseteric and hindlimb length, and lower circumanalia (Arribas 1996).

The degree of genetic differentiation between *I. c. cyreni* (Guadarrama) and *I. c. castiliana* (Gredos) was analyzed by Mayer & Arribas (2003), who found a mtDNA sequence divergence of 0.6 % in the 12s rRNA (12s) and 16s rRNA (16s) mitochondrial genes, which corresponds to approximately 0.6 MY BP. Carranza et al. (2004) suggested that both subspecies diverged approximately 0.8±0.2 MY BP, an estimation mainly based on the Cytochrome b (Cyt b) mitochondrial coding gene (the 12s and the nuclear gene C-*mos* were uninformative at this level), a divergence time almost identical to the one calculated by Crochet et al. (2004) using also the Cytb gene [1.6 % genetic divergence, which roughly corresponds to 0.6 to 1, with a mean of 0.8 MY BP). These two values were very similar to the above-mentioned ciphers. The inferred divergence time increased up to 1.2 (Cyt b) or 1.6 MY BP (Cyt b+12s) when different terminal taxa evolutionary models and phylogenetic methods were used (Arribas et al. 2006; Arnold et al. 2007; respectively).

On the other hand, specimens from Sierra de Béjar branched at the base of the *I. cyreni* clade in some mtDNA analyses (Carranza et al. 2004; Arribas & Carranza 2004). It was suggested that the split of this populations occurred approximately 1.7±0.3 MY BP (Carranza et al. 2004). However, in analyses using the same mtDNA regions but different taxa and other evolutionary models and phylogenetic methods than above (Arribas et al. 2006; Arnold et al. 2007), the specimens from Béjar formed a trichotomy with *I. c. castiliana* from Sierra de Gredos and *I. c. cyreni* from Navacerrada.

Apart from the uninformative C-*mos* nuclear gene fragment analyzed by Carranza et al. (2004) there is only one other information about differences at the nuclear level, the analysis of allozyme data by Almeida et al. (2002), which showed a Nei's distance of 0.002 between specimens from Gredos and Guadarrama.

From West to East, the distribution of *I. cyreni* can be divided into two axes connected by low mountain valleys (see appendix II), but not clearly interrupted by clear cut barriers as river valleys. One axis runs across Sierra de Béjar (summit in La Ceja, 2.425 m) and Gredos (Almanzor, 2.592 m), whereas the other axis is constituted by the Sierras de Villafranca (Moros, 2.065 m), La Serrota (Serrota, 2294 m), La Paramera (Zapatero, 2.160 m) and slightly separated by lower areas, Guadarrama (Peñalara, 2.430 m). The two axes greatly overlap longitudinally leaving the Villafranca, Serrota and Parameras just to the North of the Sierra de Gredos, but at their orographic shadow for rains, and climatically more continentalised. This explains the botanical similarities between the Paramera-Serrota-Villafranca axis and the Sierra de Guadarrama (Luceño and Vargas 1991).

In Guadarrama (where *Podarcis muralis* also exists), *I. cyreni* occurs only at the highest areas, from 1.760 m (Puerto de Cotos, Puerto de Navacerrada) up to the peaks (2.340 m in Peñalara). In Gredos it lives almost from 1.700 to 2.500 m. It was seen in 17. VII. 1986 (own data) in Puerto del Pico (at 1.352 m close to one of the fountains of the pass) but recent research in this area has been totally unfruitful. It is possible that these lower stations favoured by accelerated cold winds in the mountain passes (Venturi effect) had disappeared by climatic or best, by habitat degradation due to human over-frequentation during the last 20 years. In Béjar it has been found between 1.837 m (own data) and 2.443 m (see Lizana et al. 1988, 1992, 1993; and Martin 2005 for general data; own data corrections for the confirmed lower limits).

Apart from the better known Sierras, the presence of the Carpetane Lizard in the small parallel mountain ranges called "Sierras de Avila" or "Parameras" (composed by three Sierras: Villafranca, La Serrota, and La Paramera) was first discovered by the mountaineering group "Valle de Ambles" (Lizana et al. 1993), but no specimens have been studied so far. All aspects of morphology, status and relationships of these small and isolated populations from the Sierras de Avila are totally unknown. In these Sierras the species is extremely localized, especially in La Serrota and Paramera. In Sierra de Villafranca, the area with a relatively more extended suitable area, I have found it from 1.850 m probably up to the highest areas (Pico Moros, 2.065 m). In La Serrota it is extremely rare and localized, also cornered in the highest parts, from 2.284 m (perhaps 1.935 m where excrements, possibly of this species, were seen; pers. obs.) to the very summit (Pico Serrota, 2.294 m); and in La Paramera from 1.700 m in the northern slopes to the summit (Pico Zapatero, 2.160 m) (own data).

After a three-year prospection of these parallel ranges, I gathered data from these localized and barely known populations in order to check the relationships of all the Carpetane Lizards throughout its range. My aim is: a) to reassess differences between *I. c. cyreni* and *I. c. castiliana* in the light of the existence of other small and isolated populations; b) to ascertain the taxonomic status of the Béjar populations and to check if these represent a further subspecies; c) to study both the relationships among the samples from the Sierras de Avila (=Parameras) massifs, as well as their similitude and differences with their neighbouring and well known populations from Gredos, or the more distant populations from Guadarrama and Béjar; and d) as the type series of *I. cyreni* was destroyed during the Second World War (SWW), to choose a Neotype for the species (see appendix I) in order to fix unequivocally the type locality (although apparently all lost, there were also specimens from Gredos in the original type series).

MATERIAL & METHODS

Morphology

A total of 106/92 male specimens, and 136/135 female specimens of *I. cyreni* with a complete measurements dataset and snout-vent length greater than 45 mm, were included in the univariate (ANOVA) and multivariate (discriminant) analyses, respectively. Given that these populations present sexual dimorphism (Arribas 1996, 1999a; Arribas et al. 2006), analyses were carried out for males and females separately. All material is from Oscar Arribas (OA) database.

OTUs names, localities and specimens included in the morphological multivariate analysis were as follows (Fig. 1):

GUADARRAMA: Sierra de Guadarrama (Madrid and Segovia provinces, Spain). 25 males and 36 females [*I. cyreni cyreni*]. MIJARES: Puerto de Mijares (Sierra del Cabezo, Gredos Oriental Massif, Avila province, Spain). 6 males and 7 females. GREDOS: Circo de Gredos (Gredos Central Massif, Avila province, Spain). 23 males and 46 females [*I. cyreni castiliana*]. BÉJAR: Sierra de Béjar (Gredos Occidental Massif, also known as Sierra de Candelario, Salamanca province, Spain). 11 males and 28 females. VILLAFRANCA: Sierra de Villafranca (Avila province, Spain). 20 males and 14 females. SERROTA: La Serrota (Avila province, Spain). 3 males and 2 females. PARAMERA: Sierra de La Paramera (Avila province, Spain). 4 males and 1 female.

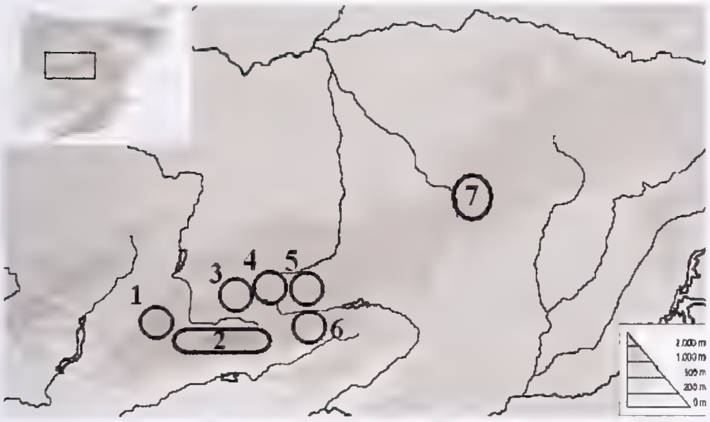

Fig. 1. Schematic representation of the distribution of *Iberolacerta cyreni* in the Spanish Sistema Central. The different localities (OTUs) cited in the text are represented. 1: Béjar; 2: Gredos; 3: Villafranca; 4: Serrota; 5: Paramera; 6: Mijares; 7: Guadarrama.

These populations are discontinuous among them (Appendix II) and constitute discrete geographical OTUs (Fig. 1).

Due to lower sample, it was necessary to cluster the Serrota and Paramera specimens in the male discriminant analysis, and these two plus Villafranca (all of them "Sierras de Avila") in the female one. However, reciprocal distances between each one of these poorly represented samples to the best represented ones were carefully checked and commented in the results section. As the three populations from Sierras de Avila seemed to be largely equivalent in the multivariate analyses, a posteriori, all of them were treated as a single OTU (Sª AVILA) in ANOVA.

Characters studied

Biometric characters. Snout-vent length (SVL); Forelimb length (FLL); Hindlimb length (HLL); Pileus length (PL); Pileus width (PW); Parietal length (PaL); Masseteric scale diameter (DM); Tympanic scale diameter (DT); Anal width (AW) and Anal length (AL). All linear measurements were made with a digital calliper to the nearest 0.01 mm. These measurements were transformed to the following more informative and not dimensional-depending ratios: FLL/SVL (relative forelimb length; "FLL index"); HLL/SVL (relative hindlinb length, "HLL index"); PL/PW (pileus shape, "Pileus index"); DM/PaL (relative masseteric plate size, "Masseteric index"); DT/PaL (relative tympanic size, "Tympanic index"); AL/AW (anal plate surface, "Anal form index") and AS/SVL (√(AL*AW)*100/SVL, relative anal plate size with respect to the total length, "Anal size index") (Arribas 1996, 2001). The results of the linear measurements and indexes yielded largely similar results. All ratios were given multiplied by 100 to avoid excessive decimal scores.

Scalation characters. Supraciliar Granula (GrS) for the right and left sides; Gularia (GUL); Collaria (COLL); Dorsalia (DORS); Ventralia (VENT); Femoralia rigth (FEMr) and left (FEMl); 4th. digit Lamellae (LAM); and Circumanalia (CIRCA).

Statistical Procedures

Statistical analyses used in the morphological study included both Univariate (ANOVA for SVL, scalation characters and indexes, with *post-hoc* Tukey-Kramer tests at $P < 0.05$ and $P < 0.01$ to detect differences among samples) as well as Multivariate techniques (Canonical Discriminant Analysis, CDA). In this later analysis, each population is represented by a centroid (a hypothetical middle individual). Minimum-length spanning tree (MST) was computed from the Mahalanobis' distance matrix to detect the nearest neighbours based on their position in the multidimensional space. MST representation also avoids distortion of UPGMA trees by the reciprocal pairwise distances recalculation in every step during their construction. UPGMA frequently clusters samples reflecting sample sizes than their true relationships. Distances of small samples or isolated specimens appear greatly exaggerated with respect to the well represented ones. As a result of that, the small-sized samples appear ever as the most external or differentiated in UPGMA derived trees (Kunkel et al. 1980; Cherry et al. 1982; Arribas 1997). Moreover, the UPGMA trees based in very unevenly sized samples also gave very poor Cophenetic Correlation Indexes between the tree-derived ultrametric distances matrix and the original Mahalanobis distance matrix and therefore we have not used them (Arribas et al. 2006).

To test the significance of the differences among pre-established groups for the Discriminant Analysis (based in a geographical origin), we carried out an Analysis of Similarity (ANOSIM) (Clark 1988, 1993) that tests if the assigned groups are meaningful, this is, more similar within groups than with samples from different groups. The method uses the Bray-Curtis measure of similarity to construct clusters of specimens. The null hypothesis is therefore that there are no differences between the members of the compared groups (they are randomly blended). R-statistic scales from +1 to -1. Values closer +1 correspond to a perfect case in which all groups were completely different (all specimens of the same group are more similar among them than to any specimens of the other groups). $R = 0$ occurs if the high and low similarities are perfectly mixed and bear no relationship to the group, a common situation if some of the groups are largely equivalent. A value of -1 indicates that the most similar samples are all outside of the groups (all groups largely equivalent and randomly formed). To check for significance, pseudoreplication tests (1000 randomizations) were run to test if the given results can occur by chance. If the value of R is significant, there is evidence that the samples within groups are more similar than would be expected by random chance. Even more important, pairwise tests among populations permit to test significance of the differences among the concerned groups and to detect which ones are really different from the others.

Mahalanobis' (squared) distance matrices were compared by means of Mantel Test (with 1000 permutations) with matrices composed by Euclidean (squared) distances for the climatic characteristics of localities: a) Precipitation (mm) during the incubation months (July and August, as scalation is invariant during lizard's life); b) Annual precipitation (mm), c) Temperature (°C) (July and August); d) Annual average temperature e) Sun radiation (n 10 kJ/(m^2*day*micrometer*)*(July and August), and f) Annual Sun radiation. Data were extracted from Ninyerola et al. (2005). Also, these Mahalanobis' distances were compared with (d) the aerial (straight) geographical distances among the sampling localities.

Multivariate (Discriminant and ANOSIM) analyses were performed with Community Analysis Package 4.0 (Henderson & Seaby 2007). MST trees and Mantel tests were calculated with NTSYS 2.1© (Rohlf 2000). Univariate statistics were processed with NCSS 2001© package (Hintze 2001).

RESULTS

Males

Canonical Discriminant Analysis. The CDA conducted with 106 male specimens shows three significant axes that explain an 85 % of the total intersample variation. The two first axes together explain the main part (70.6 %) and discriminate fairly well the samples, especially the first one, the unique with an eigenvalue >1. The first discriminant axis has an Eigenvalue of 1.54 (51.2 % of variance explained; Chi-Sq. with 85 $df = 200.71$, $P < 0.0001$) and distributes the samples with fairly overlap among them, except Guadarrama, that has only a small coincidence with the other ones (Fig. 2 A). Guadarrama appears in the negative part of the axis, characterised by the lower values for DORS (0.441553) and VENT (0.560765) and greater values of CIRCA (-0.572683). Second and third axes (eigenvalues < 1) present a considerable overlap among the samples and do not discriminate populations.

This discriminant analysis applied to the samples reached a 72.6% of correct classification among the specimens. The Guadarrama sample (*I. cyreni cyreni*) reaches a 71.9 % of correct classification in respect to all the other samples (*I. c. castiliana*).

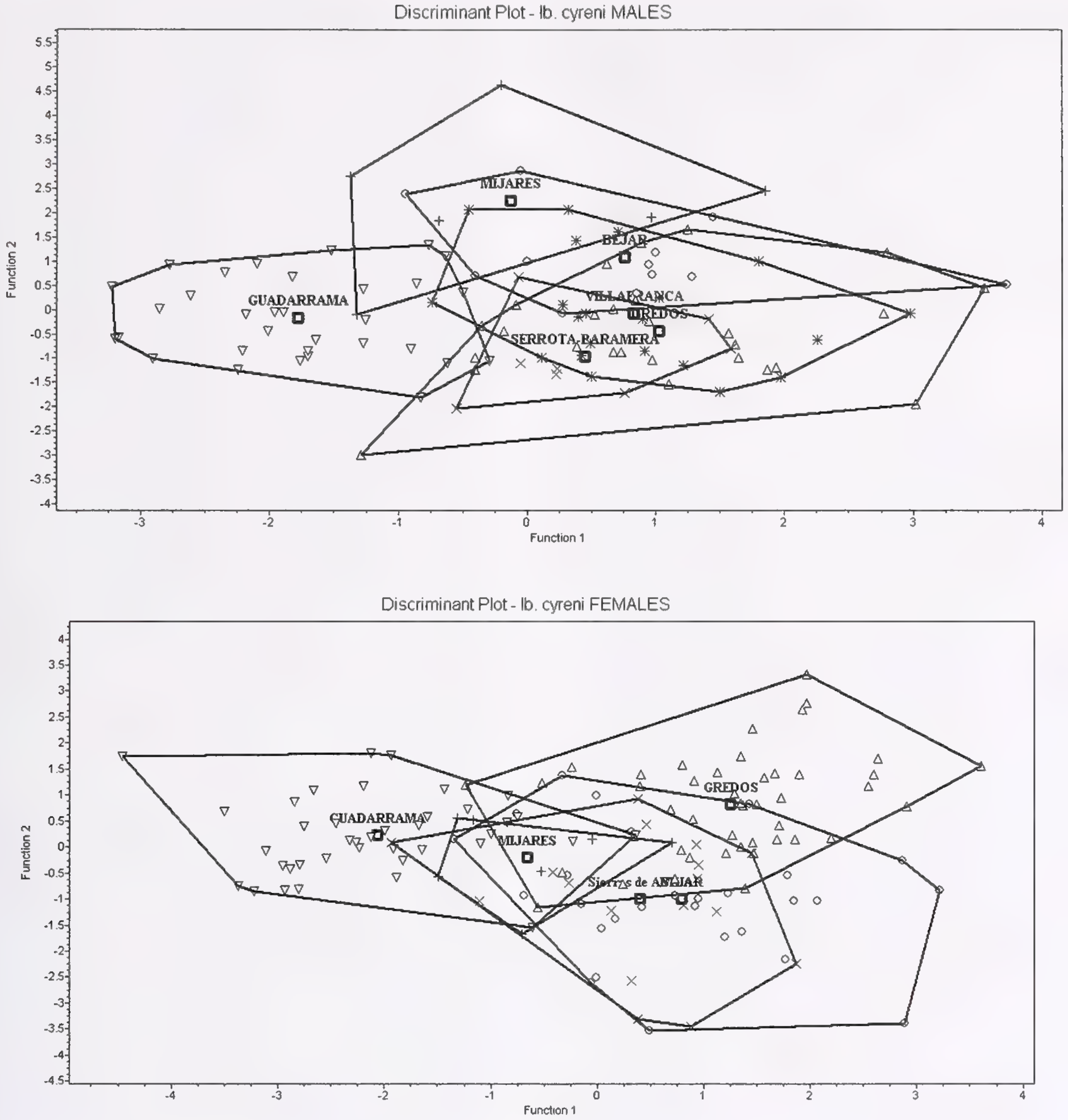

Fig. 2. Canonical Discriminant Analysis (CDA) plots for a) males (above) and b) females (below). Specimens, sample centroids and group perimeters are represented. Guadarrama (inverted triangles), Gredos (triangles), Béjar (irregular circles), Mijares (cross), Villafranca (asterisk) and Serrota-Paramera (sail). In females, the three last samples are grouped as Sierras de Avila (sail). Sample centroids are represented by a square. See text for axis characteristics and results.

Minimum-length spanning tree (not represented) connecting the centroid (hypothetical middle specimens) of each sample is fairly congruent with their geographical position, connecting in general neighbouring samples. The most "central" (most connected) population is Villafranca that connects with Gredos (at Mahalanobis Distance of 3.1870), Béjar (3.2199), Paramera (4.8042) and finally, to the most isolated one, Guadarrama (6.8412). Two populations show overestimated distances due to their small sample sizes: Mijares (East Gredos) that connects with Béjar (7.0951), and Serrota with their neighbouring Paramera (9.1822).

Analysis of Similarity (ANOSIM) (Table 3) shows that there is a considerable overlap among samples (R-statistic = 0.122088, $P < 0.005$; 1000 randomizations) as our value (that can range from 1 to -1), although positive, is very small. Very significant differences among the (geographically) assigned groups, appear only among Guadarrama and Béjar, Gredos and Villafranca ($P < 0.01$) but do not reach significance with Mijares and Serrota + Paramera (both with small samples). The other populations are not differentiated among them ($P > 0.01$).

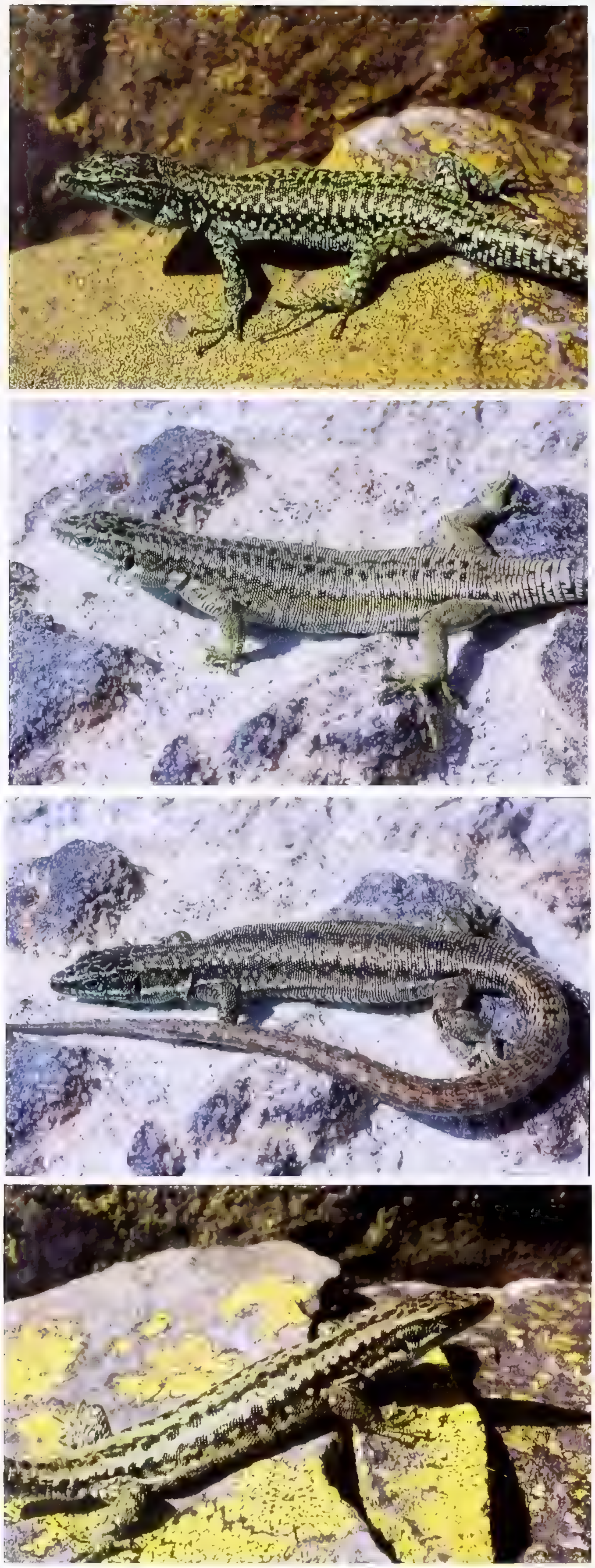

Fig. 3. *Iberolacerta cyreni castiliana*. a) La Covatilla Sky resort (Sierra de Béjar), July 2007, Male ; b) El Travieso (S^{a} de Béjar), July 2004, Female ; c) El Calvitero (Sierra de Béjar), July 2004, Female (atypical pattern, with diffumination and coalescence in a unique vertebral line); d) Puerto de Mijares (Gredos Oriental Massif), July 2006, Female.

The Analysis of Variance (ANOVA) (Appendix III, Table 1) indicate that Guadarrama differs from all or nearly all the other populations in VENT and CIRCA (with the smaller and greater values for these parameters, respectively, in the former population), but also appeared differences between Guadarrama and Béjar in Dors (smaller in the former), and with Gredos in PV (greater in the former). An interesting and significant difference appears in DORS among Gredos and Béjar samples (clearly greater in the later).

There is no significant correlation among Mahalanobis' distances and any of the geographic and climatic parameters analyzed (all Mantel Tests $P > 0.05$).

Females

Canonical Discriminant Analysis: The CDA conducted with 136 female specimens shows three significant axes that explain a 93.8 % of the total intersample variation. The two first axes together explain a large part of the variance (85.7 %), and especially along the first one, that accounts itself for 62.7 % of the total variation and is the unique with an eigenvalue >1 (1.77), discriminating Guadarrama specimens from the other neighbour samples only with a small overlap (Fig. 2B). The other samples show a considerable overlap among them. Guadarrama discriminates towards the negative part of the axis, characterised by the lower values of DORS (0.62) and VENT (0.66) and greater ones of CIRCA (-0.38). Second and third axes (eigenvalues < 1) present a considerable overlap among the samples and do not discriminate populations.

The discriminant analysis applied to the samples reached a 74.26% of correct classification among the specimens. Guadarrama sample (*I. c. cyreni*) reaches an 87.2 % of correct classification with respect all the other samples (*I. c. castiliana*).

Minimum-length spanning tree (not represented) connecting centroids is very similar to the male one. The most connected sample is Béjar, which clusters with Villafranca (at 2.9), Gredos (3.5) and Mijares (7.38, but here exaggerated by the scarce sample of the later). Guadarrama connects with the scarcely represented (and geographically intermediate) Mijares (East Gredos) (at 6.09), and all the Sierras de Avila samples cluster together (Villafranca with Serrota + Paramera at 8.66).

Analysis of Similarity (ANOSIM) (Appendix III, Table 3) shows that there is a considerable overlap among samples (R-statistic = 0.162588, $P < 0.001$; 1000 randomizations), but the results are slightly best than for the male

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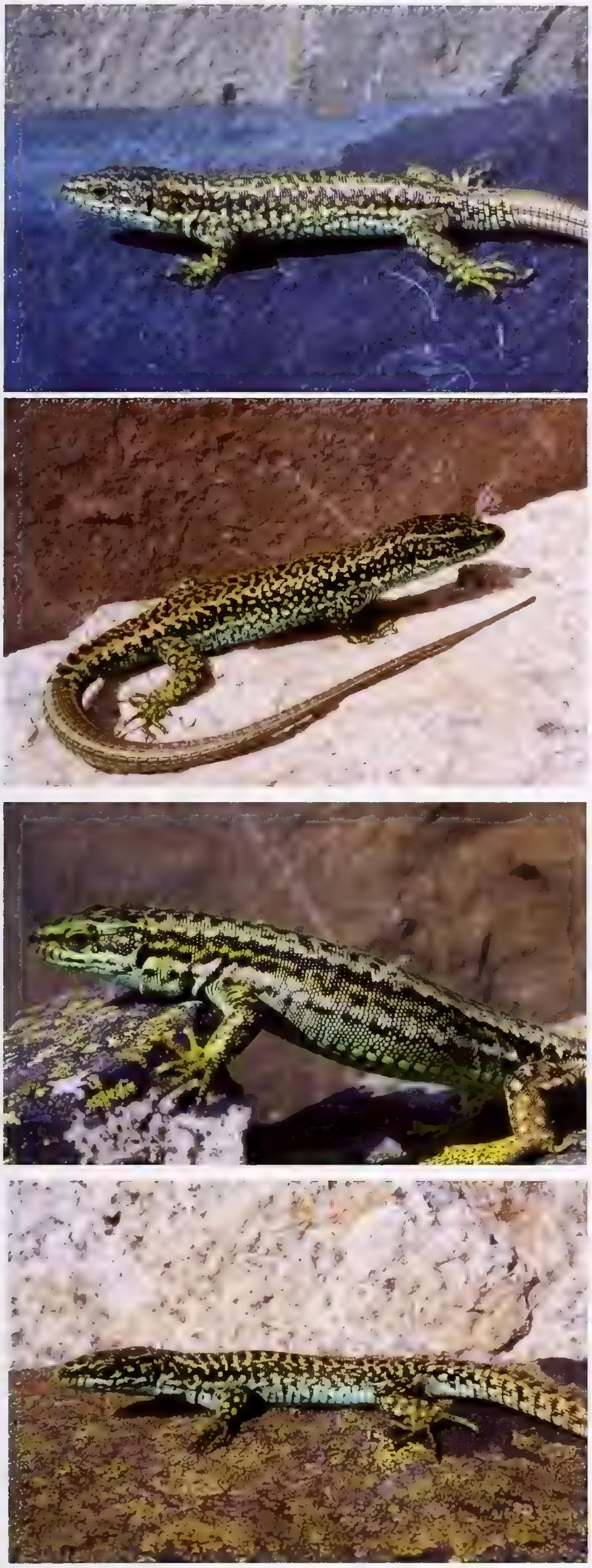

Fig. 4. *Iberolacerta cyreni castiliana*. a) Pico Zapatero (Sierra de la Paramera), July 2005, Male; b) Puerto de Peña Negra (Sierra de Villafranca), July 2006, Male; c) Pico Serrota (La Serrota Massif), July 2005, Female; d) Pico Serrota (La Serrota Massif), July 2006, Male.

analysis. Very significant differences ($P < 0.01$) appear among Guadarrama and all the other samples except with Mijares. The other populations are not differentiated among them ($P > 0.01$).

The Analysis of Variance (ANOVA) (Appendix III, Table 2), as in the male analysis, it shows that Guadarrama is the most different one, especially in DORS, VENT and CIRCA (the first two characters smaller, and the third one greater in the former population). Guadarrama also differs from Gredos by its lower GUL, from Béjar by its greater FLL, HLL, a lower SVL; and from Sierras de Avila by its greater relative anal scale surface.

Also, significant differences appear in SVL between Béjar (clearly the great sized female population) and Gredos, and among this latter (with relative greater FLL and HLL) with Béjar and Villafranca.

As in male analysis, there is no significant correlation among Mahalanobis' distances and the geographic and climatic parameters analyzed (all Mantel Tests $P > 0.05$).

DISCUSSION

From the Discriminant and ANOVA analyses it appears that the only differentiated sample is Guadarrama. It appears with very limited overlap with the other samples in the CDA graphs (Figs 2 A and B). Diagnostic characters for this population (nominate subspecies: *I. c. cyreni*) are the lower values of DORS (difference more marked in females), lower values of VENT and greater CIRCA. Moreover, ANOSIM analyses show that Guadarrama is the unique OTU that is significantly different from nearly all the other samples, except from the close population of Mijares (in both sexes) and Serrota + Paramera (but these exceptions occur only in the males and probably due to their scarce sample size).

Mijares sample (very small) seems in some aspects approaching to Guadarrama (specially in DORS and VENT values) but globally are clearly closer to *I. c. castiliana* (specially to Béjar in male and female MST).

Populations West from Guadarrama show a great overlap in CDA and lack differences in ANOSIM, being morphologically fairly equivalent and all of them assimilable to *I. c. castiliana*. There are only a few scattered very significant differences among them ($P < 0.01$) in ANOVA, as for instance among Gredos and Béjar (this latter has greater DORS and a strikingly greater SVL and proportionally shorter limbs that Gredos, but only in female specimens). The reason of the longer SVL in Béjar females (from 8 mm to 1 cm greater than in the other populations) which leaves proportionately shorter limbs, can be a consequence of body elongation that in lacertids appears linked to a greater clutch size (Braña 1996). This is an interesting question for future study: if Béjar specimens effectively have greater clutch size that other *I. cyreni* populations.

Both the MST results (in which Villafranca and Béjar are the most connected samples) as well as the presence of related species further West (*I. martinezricai* and *I. monticola*), suggest an origin of the species towards the western extreme of their current distribution area. From these westernmost parts, where it also occurs the higher haplotype diversity (see below), *I. cyreni* spread towards the East. Despite that the Sierras de Avila (Villafranca, Serrota and Paramera) are slightly more aligned with the Guadarrama axis than with Gredos one, we cannot be sure from which of these two mountain ranges the former was colonized, as MST results in males and females are contradictory. According to the male analysis Guadarrama is more related to Villafranca, whereas in the female analyses, it is Mijares (Eastern Gredos) the most related one.

The results of the mitochondrial analyses of these samples (Cyt B and 12s) (unpublished, Carranza, pers. com.) indicates that the interruption of gene flow is fairly recent, as a common haplotype appears in all populations except Villafranca and Béjar. All Gredos, Guadarrama and La Serrota specimens are identical for these two mitochondrial fragments. Independent changes in one nucleotide with respect to the common haplotype appear in Villafranca (the unique change is different in two specimens), Paramera, Mijares and Béjar specimens, and two changes accumulate in one Béjar and one Mijares specimen (others have only one).

The current morphological differences of Guadarrama specimens seem to be relatively recent, and are possibly the result of bottleneck effects during the colonization process, or alternatively of strong selective pressures (or a combination of both causes). Conversely, the absence of marked differences among the other populations (more or less with a similar age) could be due to the maintenance of a more continuous gene flow among them, responsible of maintaining their morphology largely equivalent (nuclear genes remain unstudied). The current larger geographical gap in the distribution of *I. cyreni* occurs precisely between Guadarrama and the remaining populations to the West.

Despite the presumably short isolation time, as commented above, a considerable selection pressure or a genetic bottleneck in the expanding populations might have promoted and fixed the morphological differences now seen in Guadarrama specimens. These factors do not seem to be due to isolation-by-distance processes but by historical vicariant events (cf. Irwin 2002) as there is no relationship between morphological differentiation and geographic distances. Also there is no relationship among the more obvious climatic parameters (precipitation, temperature and sun radiation) and these differences.

Concerning the position of Béjar populations, only specimens from the west-facing slopes of the massif have been studied, and therefore it is possible that in other parts of the massif other haplotypes (the common one with Gredos) could be present. The species was cited from "Puerto de Tornavacas, SA" (for Salamanca, sic.!; a mistake as this locality is in Avila) (Lizana et al. 1992). This is the natural pass between Béjar and Gredos, but I have been unable to find it there. This place is a sub-Mediterranean environment with Pyrenean Oak open forest inhabiting populations of *Timon lepidus*, *Psammodromus algirus* and even *Buthus occitanus*, all thermophylous species typical from dry conditions. The lower height of Puerto de Tornavacas (1010m) makes me to suspect that *I. cyreni* is not there and the record is possibly a mistake. One possibility is that it was from the higher neighboring mountains.

An account about the pattern and coloration of *I. cyreni* is in Arribas (1996) and it is especially detailed for the main Sistema Central massifs in Perez-Mellado et al. (1993). Both colour as well as the dark pattern, seem to be selected in accordance to the substrate characteristics. Overall, the background colour is brown in juveniles and subadult specimens, changing in different percentages to green in adult specimens (more frequently in males and becoming more vividly linked to reproductive processes). In populations inhabiting rocks (plenty of *Rhizocarpon* gr. *geographicum* lichens) as in Gredos and the upper parts of Guadarrama (Peñalara) green adults are more frequent (both males and big females). When living in rocky talus with sands and bare ground (as in Navacerrada area) brownish adult specimens are more frequent (Arribas 1999b: Figs 9 and 10).

Concerning the reticulate pattern, it also varies in a different degree among the different populations depending on the substrates inhabited. Juveniles and subadults have temporal uniform or reticulate bands that coalesce during growth with dorsal spots (more frequently in males) giving reticulated-like patterns. Usually, there is a relationship between the size of the granite phanerocrystals (the granite-rock spotting) and the habitus of the lizards living on it. Lizards living on rocks that present large crystals (as for instance the Béjar ones) are more reticulated than specimens living in places in which the rocks present smaller crystals (and thus finely spotted). Coloration accounts described in Perez Mellado et al. (1993) are fairly precise, especially for Gredos specimens. Concerning

Béjar (=Candelario in Perez Mellado et al. [1993]) the description should be corrected as, although it is true that very old specimens are fairly reticulated, especially males, females more frequently have two paravertebral rows of distinctive spots (photo 2), as in females of other populations and in mid-grow specimens of both sexes in all localities. The statement that "the most common background colour of the back and flanks is greenish or bluish" probably is true for fully adult specimens during the breeding period, but in July and August only some big males conserve greenish tones, appearing even fully adult females more or less brownish.

Concluding: a) *I. c. cyreni* is a recently differentiated but well diagnosable (morpho)subspecies, a case paralleling the relationship of *I. monticola monticola* from Serra da Estrela (Portugal) with repect to *I. m. cantabrica* (from Galicia and Cantabrian Mts.), in this later case, with no genetic differences, but with singular morphological traits that distinguishes it from other *I. monticola* in a multivariate analysis (Arribas & Carranza 2004; Arribas et al. 2006). Highly variable nuclear markers as for instance introns or microsatellites may help to clarify definitively the status of these well diagnosable (morpho)subspecies.

b) Despite the mtDNA differences of the Béjar specimens (one or two nucleotides), their morphology is largely equivalent to *I. c. castiliana*. Lacking data from other Béjar populations and genetic nuclear markers, I assume that these morphological similarities reflect the presence of a very recent gene flow with other neighbouring populations. The Béjar populations are however outstanding by their female body elongation (up to near 1 cm larger), conserving proportionately shorter limbs, which can be a strategy to increase clutch size.

c) The Sierras de Avila populations are very similar; the closer among all the populations compared. One of them, the Sierra de Villafranca, is together with Béjar, the most connected sample, and it is, from a morphological point of view, at the root of the species expansion. Both also present the unique slightly variant haplotypes. All they should be considered as *I. c. castiliana* by their closer identity with Gredos.

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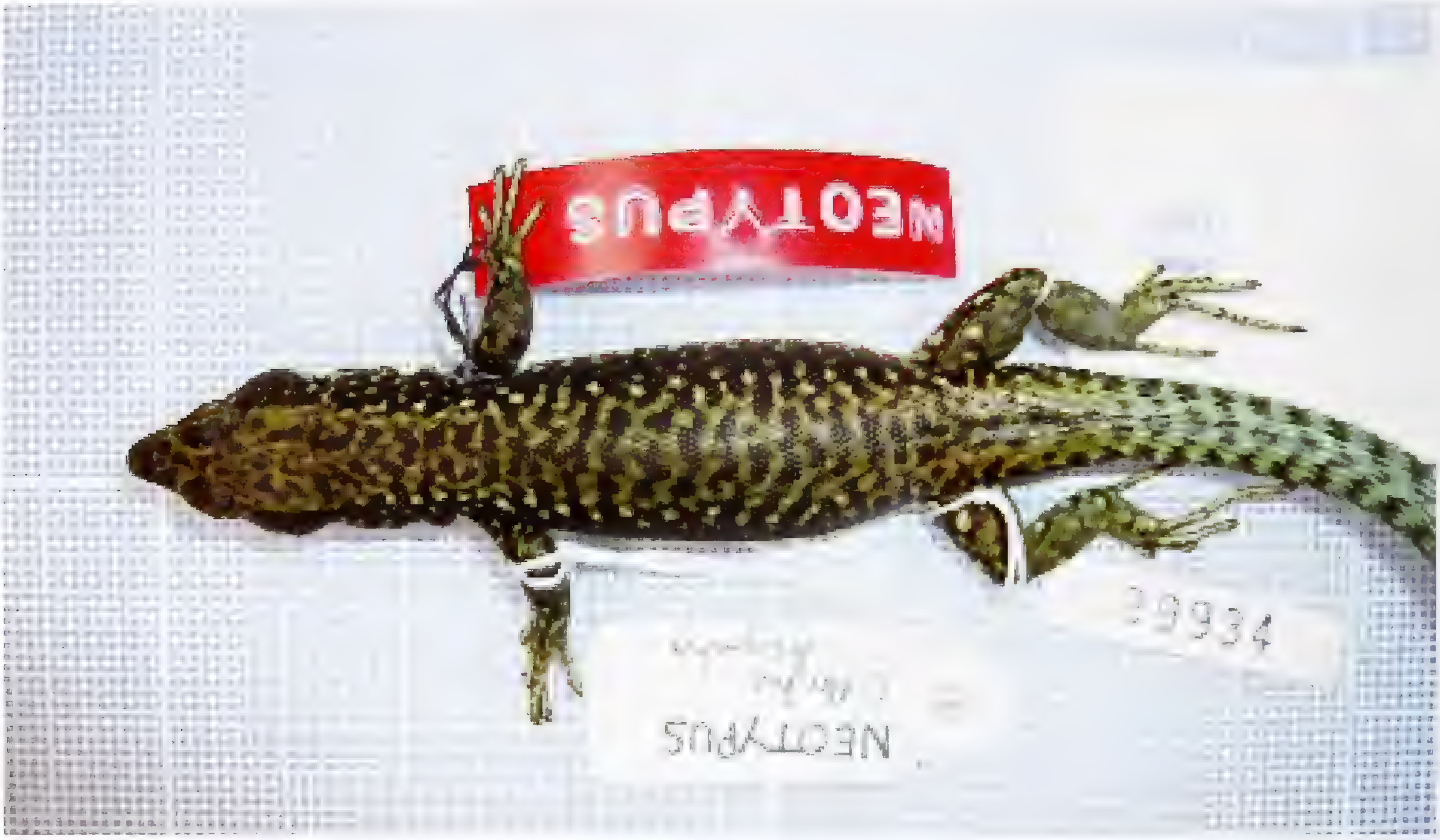

Fig. 5. *Iberolacerta cyreni* NEOTYPE (here designed). MNCN n. 39934.

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APPENDIX I

Neotype designation for *Iberolacerta cyreni* (Müller & Hellmich, 1937)

The type series of *Iberolacerta cyreni* (*Lacerta monticola cyreni* Müller & Hellmich, 1937) included 66 specimens (not only from Guadarrama, the species' type locality, but also some paratypes from Gredos) formerly deposited in the Zool. Staatssamlung (Herpet. Samml.) München. In fact, two syntype specimens, male and female, respectively numbered "ZSM (SLM) 2329 a" and "ZSM (SLM) 2329 b", were originally considered as types labelled "Guadarrama, Puerto de Navacerrada. W. Hellmich". (Müller & Hellmich, 1937).

Although it seems that all the original type series was destroyed during the Second World War (Franzen & Glaw, 2007), and due to the fact that in this type series there were included some Gredos specimens (today part of another subspecies; *I. c. castiliana*), and also that there was early confusion about the *I. monticola* type locality which lead to the description of a new taxon as *Lacerta estrellensis* Cyren, 1928 (Arribas 2008), I design a new type specimen (neotype) to fix unequivocally the type locality against any contingence (as could be the highly improbable apparition of any "surviving" original Gredos paratype).

I designate here as NEOTYPE for the species a specimen from the Museo Nacional de Ciencias Naturales (Madrid) (MNCN n. 39934) (Fig. 5).

A male labelled as follows:

Left hindleg: (white label, Typewriter letter) MNCN (anverse), 39934 (reverse).

Right hindleg: (white label, pencil handwritten) "Pto. de Cotos–Pto de Navacerrada. Srra. de Guadarrama ( )[blank inside parenthesis], 21–IV–84, 18,15 h. Sol. Pedriza en pinar con nieve. Ps=8.5 gr." (no collector's data).

Left foreleg: (White label, ink handwritten) Neotypus. O. Arribas designatio (anverse), "*Lacerta monticola cyreni* Müller & Hellmich, 1937" (=*Iberolacerta cyreni*) (reverse).

Right foreleg: (Red plastic label, Dymo® lettering) NEOTYPUS.

Neotype description (Fig. 5):

Biometry: Adult male with snout–vent length of 66.85 mm. Tail 126 mm (intact). Forelimb length 23.34 mm. Hindlimb length 34.52 mm. Pileus length 16.4 mm. Pileus width 8.2 mm. Parietal legth 5.5 mm. Masseteric widest diameter 2.71 mm. Tympanic widest diameter 1.94 mm. Anal plate width 5.04 mm. Anal length 3.19 mm. FLL/SVL (relative forelimb length): 0.349. HLL/SVL (relative hindlimb length): 0.5163. PL/PW (pileus shape): 2.003. DM/PaL (relative masseteric plate size): 0.491. DT/PaL (relative tympanic size): 0.352. AL/AW (anal plate surface): 0.6329. AS/SVL (relative anal plate size in respect to total legth): 5.998.

Scalation: Number of supraciliary granules: 9 (rigth) and 11 (left). Supralabials: 5 (both sides). Sublabials: 6 (right side) and 7 (left side). Submaxillars: 6 (both sides). Gularia: 25. Collaria: 9. Dorsalia: 53. Ventralia: 26. Femoral pores 19 (right) and 18 (left). Lamellae: 25. Circumanal Plates: 8. Rostral in full contact with frontonasal. Supranasal separated from first loreal. One postnasal (in both sides). First Postocular separated from Parietal plate. Alternate wide and narrow scale rings in the tail. Twenty–six scales across one of these rings.

Coloration: (in alcohol). Dorsal tract and pileus brown (probably also in life), densely spotted of medium–sized black spots that in the middle of the dorsum nearly form transverse bands and connect the two temporal bands. Temporal bands reticulated fairly dark (black–brown) with traces of clear occelli (barely visible) inside, also connecting with more light reticulated with infratemporal band (barely discernible). No blue axillar occelli. Traces of blue points in the outermost ventral scales. Only the outermost ventral scale ranges are clearly black spotted. Belly light bluish or white–bluish.

APPENDIX II

Barriers and high mountain passes (among parentheses) between the different *I. cyreni* populations. All these intermediate areas are at present apparently devoid of *I. cyreni*, thus constituting these OTUs discrete populations:

BÉJAR–GREDOS: no barrier (Puerto de Tornavacas, 1275m).

BÉJAR–VILLAFRANCA: Tormes River Valley (no pass).

GREDOS–VILLAFRANCA: Tormes River Valley (Collado de Cepegato, 1550m).

GREDOS–S^a AVILA[Serrota+Paramera]: Alberche River Valley (no passes).

SERROTA–PARAMERA: no barrier (Puerto de Menga, 1566m).

VILLAFRANCA–SERROTA: no barrier (Puerto de Chia, 1663m).

S^a AVILA (as a whole) – GUADARRAMA: no barrier (Puerto del Boquerón, 1315m).

GREDOS–GUADARRAMA: Alberche River Valley (no pass)

APPENDIX III

Table 1. ANOVA and descriptive statistics (mean, standard error, minimum and maximum) from morphometric, scalation and biometrical indexes of *I. cyreni* male samples. See Material and Methods text for abbreviations of characters and indexes used in the morphometric analysis.

MALES	GUADARR. (1) (n=25)	MIJARES (2) (n=6)	GREDOS (3) (n=23)	BEJAR (4) (n=11)	Sª AVILA (5) (n=27)	$F_{4,87}$	p	1–2	1–3	1–4	1–5	2–3	2–4	2–5	3–4	3–5	4–5
SVL	61.85±1.76	56.09±4.12	66.34±1.37	64.23±3.21	63.43±1.79	1.90	0.118272										
	45.1–74.5	48.17–71.37	49.9–72.4	48.3–77.38	45.12–74.91												
GrS r	10.4±0.37	10.83±0.79	11.26±0.55	11.36±0.85	11.22±0.37	0.67	0.616208										
	6–13	9–14	7–18	6–15	8–16	1.29	0.279781										
GrS l	10.52±0.36	11±0.85	10.43±0.46	11.63±0.66	11.44±2.15												
	7–15	9–15	7–16	8–15	8–17												
GUL	24.04±0.36	23.66±0.42	25.30±0.44	25.36±0.62	23.81±0.33	3.14	0.018460										
	21–27	22–25	23–31	23–29	20–28												
COLL	10.44±0.20	12.16±0.40	10.73±0.26	10.45±0.28	10.25±0.19			**				*	*	**			
	8–12	11–13	7–13	9–12	8–13	4.03	0.004827										
DORS	49.64±0.55	52.5±1.28	51.21±0.70	55.18±1.22	52±0.57	6.15	0.000209			**					**		*
	45–56	50–57	46.57	50–64	46–57												
VENT	24.6±0.2	25.66±0.33	26.08±022	25.9±0.36	26.14±0.22	8.28	0.000010		**	*	**						
	23–26	25–27	24–29	24–28	24–29												
FEM r	18.72±0.31	18.83±0.30	18.3±0.34	19.18±0.55	18.07±0.29	1.27	0.287378										
	16–22	18–20	15–22	17–24	15–22												
FEM l	18.56±0.28	18.5±0.34	18.13±0.36	18.72±0.70	18.07±0.26	0.58	0.678824										
	16–21	18–20	14–22	16–24	16–22												
LAM	25.2±0.33	26±0.96	25.13±0.43	26.27±0.4	24.85±0.36	1.40	0.241656										
	22–29	23–29	21–29	24–29	21–30												
CircA	8.2±0.20	6.83±0.30	6.63±0.21	7±0.26	7.4±0.17	8.85	0.000005	*	**	**	*					*	
	6–12	6–8	5–9	6–9	6–9												
R–I	1.88±0.06	2±0	1.82±0.10	1.90±0.09	1.88±0.06	0.31	0.869978										
	1–2	2–2	0–2	1–2	1–2												
Po–Pa	0.2±0.08	0±0	0.15±0.09	0.13±0.09	0.24±0.06	0.58	0.680982										
	0–1	0–0	0–2	0–1	0–1												
Sn–Lor	0±0	0.16±0.16	0±0	0.04±0.04	0.07±0.04	1.84	0.127894										
	0–0	0–1	0–0	0–0.5	0–1												
PV	1.12±0.17	1.33±0.42	0.43±0.12	0.72±0.19	0.85±0.07	4.07	0.004509		**			*					
	0–3	0–3	0–2	0–2	0–1												
FLL/SVL	36.24±0.003	34.54±0.004	35.46±0.006	35.03±0.004	34.55±0.003	2.52	0.046941				*						
	30.81±39.91	32.83–35.66	29.22–42.37	32.77–37.01	31.95–38.94												
HLL/SVL	51.46±0.004	50.27±0.004	50.96±0.005	50.62±0.004	50.87±0003	0.69	0.602439										
	46.39–56.34	48.49–51.20	43.93–55.19	49.01–53.15	47.89–54.59												
PL/PW	216.03±0.02	214.28±0.04	211.42±0.04	225.32±0.11	214.47±0.02												
	195.45–231.34	199.14–228.20	120.16–226.31	197.48–338.30	191.53–235.88	1.06	0.380913										
DM/PaL	38.33±0.009	37.88±0.02	42.12±0.01	39.97±0.03	44.11±0.01	3.24	0.015768										
	30.90–50.36	30.97–46.21	32.30–53.84	16.57–55.86	29.49–53.78												
DT/PaL	35.25±0.01	33.22±0.02	36.09±0.01	37.97±0.02	35.37±0.009	0.77	0.550028										
	21.81–48.83	22.52–39.36	27.5–49.18	29.1–56.1	28.61–47.2												
AL/AW	55.22±0.01	62.54±0.03	59.59±0.01	58.33±0.02	59.41±0.009												
	45.83–66.66	55.01–71.61	40.81–81.48	45.23–68.55	49.71–71.54	2.36	0.059363										
AS/SVL	566.31±0.11	509.68±0.28	546.24±0.11	522.42±0.08	563.25±0.08	2.74	0.033479										
	436.00–689.68	449.53–639.73	449.13–662.44	474.43–566.42	473.26–639.11												

Table 2. As in table 1, but for *I. cyreni* females.

FEMALES	GUADARR (1) (n=36)	MIJARES (2) (n=7)	GREDOS (3) (n=46)	BEJAR. (4) (n=28)	Sª AVILA (5) (n=16)	$F_{4,129}$	P	1–2	1–3	1–4	1–5	2–3	2–4	2–5	3–4	3–5	4–5
SVL	64.68±1.45 48.02–79.72	63.57±3.43 48.41–72.34	64.57±0.85 49.4–73.6	73.62±1.15 50.28–81.74	66.52±3.08 47.54–81.33	7.13	0.000032			**			*		**		*
GrS r	9.8±0.22 8–13	9.57±0.42 8–11	10.86±0.28 5–17	10.53±0.29 8–15	11.25±0.51 8–14	3.39	0.011398		*		*						
GrS l	9.88±0.29 6–13	10.14±0.55 8–12	11.08±0.28 5–16	10.64±0.31 8–16	11.18±0.47 8–15	2.88	0.025101		*								
GUL	23.63±0.30 19–27	24±0.78 21–27	25.65±0.34 22–33	24.71±0.37 21–29	23.75±0.42 20–26	6.06	0.000167		**				*			*	
COLL	10.33±0.19 8–14	10.14±0.26 9–11	10.34±0.15 9–13	10.28±0.2 8–12	10.87±0.23 9–13	1.03	0.394934										
DORS	47.61±0.52 43–54	50.42±1.06 47–54	52.21±0.45 47–59	52±0.53 47–59	50.43±0.65 45–55	14.17	0.000000		**	**	*						
VENT	27.75±0.16 25–29	27.85±0.50 26–30	29.04±0.16 26–31	29.32±0.19 27–31	29.62±0.24 27–31	15.35	0.000000		**	**	**		*	**			
FEM r	17.91±0.28 14–21	17.85±0.14 17–18	17.82±0.25 15–22	18.02±0.33 15–21	17.31±0.28 15–19	0.57	0.681349										
FEM l	17.63±0.27 15–22	17.85±0.14 17–18	17.91±0.2 15–20	17.96±0.25 15–20	17.12±0.30 14–19	1.17	0.328219										
LAM	23.91±0.26 21–27	24.28±0.47 23–26	24.82±0.27 20–29	25±0.25 22–27	24.31±0.37 22–27	2.50	0.045761										
CircA	8.41±0.12 7–10	6.71±0.52 5–9	7.08±0.15 5–9	7.46±0.19 6–9	7.25±0.26 6–9	11.55	0.000000	**	**	**	**						
R–I	1.55±0.12 0–2	1.71±0.28 0–2	1.73±0.09 0–2	1.60±0.13 0–2	1.56±0.18 0–2	0.41	0.802233										
Po–Pa	0.38±0.11 0–2	0.28±0.18 0–1	0.55±0.11 0–2	0.39±0.10 0–2	0.46±0.11 0–1	0.56	0.691754										
Sn–Lor	0.08±006 0–2	0.14±0.09 0–0.5	0.21±0.07 0–2	0.14±0.06 0–1	0.12±0.07 0–1	0.52	0.721220										
PV	0.47±0.1 0–2	0.42±0.2 0–1	0.26±0.07 0–2	0.39±0.16 0–3	0.43±0.15 0–2	0.73	0.571095										
FLL/SVL	33.15±0.003 29.74–36.45	31.39±0.008 28.54–34.54	33.34±0.003 27.93–39.68	30.57±0.004 27.42–35.81	30.93±0.006 26.7–34.13	9.42	0.000001			**	*				**	**	
HLL/SVL	45.94±0.005 40.10–52.33	46.34±0.008 44.32–51.20	47.19±0.005 37.82–52.75	43.45±0.005 37.83–49.08	44.0±0.008 38.36–49.21	7.96	0.000009			*					**	**	
PL/PW	208.92±0.01 194.22–227.88	205.32±0.02 197.09–219.20	212.03±0.02 132.4–234.7	214.46±0.02 192.70–229.86	206.53±0.02 190.10–219.04	2.31	0.061733										
DM/PaL	36.76±0.01 28.00–50.21	38.02±0.02 28.02–48.67	39.71±0.01 25.53–51.03	40.87±0.01 24.74–57.46	41.38±0.02 18.51–52.44	2.23	0.069286										
DT/PaL	34.78±0.007 22.41–41.9	38.52±0.01 35.23–43.76	35.40±0.08 22.72–46.93	39.45±0.01 24.31–49.84	37.78±0.01 30.84–46.6	4.14	0.03469			**					*		
AL/AW	56.73±0.01 46.03–101.88	58.75±0.02 49.90–65.12	57.64±0.008 37.25–68.29	60.10±0.013 47.52–75.16	58.85±0.01 50.00–66.99	1.06	0.376996										
AS/SVL	553.60±0.07 448.7–585.37	494.73±0.17 476.36–740.81	524.29±0.06 404.59–544.34	530.21±0.01 445.33–634.58	507.42±0.10 415.06–624.84	4.69	0.001449	*	*		**						

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Table 3. Analysis of Similarity (ANOSIM) results (with 1000 randomizations). Males above diagonal and females below. The number is the test probability results among each two concerned populations (significant results in bold).

FEM \ MAL	BÉJAR	GREDOS	GUAD.	MIJARES	SERR-PAR	VILLAFR.
BÉJAR	–	0.058	**0.001**	0.644	0.138	0.064
GREDOS	0.021	–	**0.001**	0.691	0.867	0.198
GUAD.	**0.001**	**0.001**	–	0.097	0.128	**0.001**
MIJARES	0.53	0.039	0.327	–	0.224	0.513
SERR–PAR	0.127	0.025	**0.001**	0.217	–	0.86

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Insights into chameleons of the genus *Trioceros* (Squamata: Chamaeleonidae) in Cameroon, with the resurrection of *Chamaeleon serratus* Mertens, 1922

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Abstract. Relationships among chameleons of the genus *Trioceros* in Cameroon are reviewed on a molecular basis using mitochondrial genes and by morphology. *Trioceros oweni* is placed basal to two distinct clades (lowland-submontane species vs. submontane-montane species) and its position is discussed due to high genetic differences to the remaining taxa. Within the lowland-submontane species group, distinct subclades with low genetic differences exist within *T. montium* and *T. cristatus*. Differing relationships to previously published results are observed within the submontane-montane species group, resulting in taxonomic changes: *Trioceros eisentrauti* is grouped with the two *T. quadricornis* subspecies, showing only low genetic differences, which also correlates with the similar overall morphology. The taxon is thus assigned to a subspecific rank: *T. quadricornis eisentrauti*. Within the *wiedersheimi*-group, the former southern subspecies is elevated to species rank, *Trioceros perreti*, and two additional species have been distinguished by molecular and morphological methods in the former nominate taxon. *Trioceros wiedersheimi* is restricted to northernmost localities, while remaining populations have been assigned to the revalidated taxon *Trioceros serratus* (Mertens, 1922). Differentiating morphological characters for the three species are provided and a neotype of *Chamaeleon serratus* Mertens, 1922 is designated and described to ensure clarification of its taxonomic status and type locality.

Key words. Reptilia, Chamaeleonidae, *Trioceros*, *Trioceros serratus*, Africa, Cameroon, phylogeny, taxonomy.

INTRODUCTION

Only recently, Tilbury & Tolley (2009) provided molecular evidence that the two former subgenera (*Chamaeleo* Laurenti, 1768 sensu stricto and *Trioceros* Swainson, 1839) of the chamaeleonid genus *Chamaeleo* as recognized by Klaver & Böhme (1986) represent two distinct and valid genera. For a diagnosis of the two genera see Klaver & Böhme (1986, 1992) and Tilbury & Tolley (2009). Klaver & Böhme (1992) additionally provided a detailed overview of formerly published knowledge on the *cristatus*-subgroup inside the *Trioceros*-group from Cameroon.

The Republic of Cameroon exhibits a very high diversity of chameleon species compared to adjacent countries, especially in montane areas (Böhme & Klaver 1981; Gonwouo et al. 2006; Herrmann et al. 2005, 2006). At present 14 species of chameleons are known to occur in Cameroon. They belong to the genera *Chamaeleo* [five

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species: *C. africanus* Laurenti, 1768; *C. dilepis* Leach, 1819; *C. gracilis* Hallowell, 1842; *C. quilensis* Bocage, 1886; *C. senegalensis* Daudin, 1802], *Rhampholeon* [one species: *R. spectrum* (Buchholz, 1874)] and *Trioceros* [eight species: *T. camerunensis* (Müller, 1909); *T. cristatus* (Stutchbury, 1837); *T. eisentrauti* (Mertens, 1968); *T. montium* (Buchholz, 1874); *T. oweni* (Gray, 1831); *T. pfefferi* (Tornier, 1900); *T. quadricornis* (Tornier, 1899); *T. wiedersheimi* (Nieden, 1910)]. *Trioceros quadricornis* and *T. wiedersheimi* are polytypic, with one more subspecies [*T. q. gracilior* (Böhme & Klaver, 1981), *T. w. perreti* (Klaver & Böhme, 1992)], resp. (Böhme & Klaver 1981; Chirio & LeBreton 2007; Gonwouo et al. 2006; Klaver & Böhme 1986; Tilbury & Tolley 2009). According to Klaver & Böhme (1997) and Uetz & Hallermann (2010) one additional species (*Chamaeleo laevigatus* Gray, 1863) is present in Cameroon, but this species has not been listed by other recent authors (Chirio & LeBreton 2007; Gonwouo et al. 2006; Tilbury 2010). While some species such as *Chamaeleo gracilis* or *Trioceros cristatus* show a large distribution ranging at least from Nigeria to Gabon and the Congo (Nečas 2004), five species are regarded as montane endemics occupying restricted high elevation areas along the Cameroon mountain chain, with *T. eisentrauti* the most restricted, being endemic to the Rumpi Hills in western Cameroon (Chirio & LeBreton 2007; Gonwouo et al. 2006; Klaver & Böhme 1992).

Pook & Wild (1997) published a preliminary phylogeny of *Trioceros* from Cameroon, and we herein provide additional and new insights into this species group based on additional material.

MATERIAL AND METHODS

In all, 49 combined, mitochondrial 16S and 12S rRNA gene fragments, sequences (Tab. 1, Appendix II; museum acronyms see below) comprising 964 bp (lengths referring to the aligned sequences including gaps) were obtained. One short section (4 bp from the 12S gene) was too variable to be reliably aligned, and was excluded from the analyses, resulting in a total of 960 bp which were used in the analyses. *Kinyongia tavetana* (AM422414/AM422433; Mariaux et al. 2008) was used as outgroup. Its position outside of *Trioceros* was demonstrated by Tilbury & Tolley (2009). DNA was extracted using QiAmp tissue extraction kits (Qiagen) and the peqGold Tissue DNA Mini Kit (PEQLAB Biotechnologie GmbH) (see Wagner et al. 2009a). The primers 16sar-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr-H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of Palumbi et al. (1991) were used to amplify a portion of the mitochondrial 16S ribosomal RNA gene. Additionally, a section of the mitochondrial 12S ribosomal RNA gene was amplified using the primers 12SA-L (light chain; 5' – AAA CTG GGA TTA GAT ACC CCA CTA T – 3') and 12SB-H (heavy chain; 5' – GAG GGT GAC GGG CGG TGT GT – 3') of Kocher et al. (1989). PCR cycling procedures were as described in Schmitz et al. (2005). PCR products were purified using Qiaquick purification kits (Qiagen). Sequences were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (Thompson et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall 1999). PAUP* 4.0b10 (Swofford 2002) was used to compute the uncorrected pairwise distances for all sequences (Tab. 2, Appendix II). We performed neighbour-joining (NJ), maximum parsimony (MP), maximum likelihood (ML) and Bayesian reconstructions. For ML and Bayesian analysis parameters of the model were estimated from the data set using Modeltest 3.7 (Posada & Crandall 1998) and MrModeltest 2.3 (Nylander 2002), respectively. For the MP analysis, we used the "heuristic search" with the "random addition" option of PAUP* (Swofford 2002) with 10 replicates, using the TBR (tree bisection-reconnection) branch swapping option. For the ML tree we used the PhyML 3.0 computer cluster of the Montpellier bioinformatics platform (http://www.atgc-montpellier.fr/phyml/) (Guindon & Gascuel 2003). All Bayesian analyses were performed with MrBayes, version 3.12 (Huelsenbeck & Ronquist 2001). The exact parameters used for the Bayesian analyses followed those described in detail by Reeder (2003). For the Bayesian reconstruction clades with posterior probabilities (PP) ≥ 95% were considered strongly (significantly) supported. Additionally, we used bootstrap analyses with 1000 (for ML), 2000 (for MP) and 20000 (for NJ) pseudoreplicates to evaluate the relative branch support in the phylogenetic analysis.

In the morphological analysis measurements follow standard procedures (e.g.Werner 1902; Mariaux et al. 2008) and were taken on preserved material with an electronic dial calliper (± 0.1 mm). All measurements are given in mm (Tab. 3, Appendix II). Analysis of morphological data has been performed using PAST software (Version 1.82b; Hammer et al. 2001). If measurements (e.g. femur length) differed between body sides, mean values were used. Photos of living specimen have been used to analyse colouration patterns.

Investigated specimens are deposited in Muséum d'histoire naturelle, Geneva (MHNG); Muséum national d'Histoire naturelle, Paris (MNHN); National Museum, Museum of Natural History, Prague (NMP6V); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin (ZMB); Zoologische Staatssammlung München (ZSM).

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RESULTS

To date ten taxa belonging to the genus *Trioceros* have been recognized in Cameroon (eight species + two subspecies), but the present phylogenetic analysis is inconsistent with this arrangement (Fig. 1). All four used phylogenetic methodologies strongly agree in the overall topology and in all cases support the same terminal clades. The phylogenetic analyses reveal only a single difference (discussed below) for the individual analysis of the two applied gene fragments (not shown), therefore, we only discuss the results of the combined analysis.

Distances between ingroup and outgroup species averaged 11.48% (10.58%–12.30%; Tab. 2, Appendix II). Interspecific distances within the ingroup ranged from 3.21%–6.90% excluding *T. oweni.*

Trioceros oweni is the most basal taxon in respect to all ingroup taxa, which are grouped within one clade fully supported in NJ, MP and ML, while still strongly, but not fully significantly supported in the Bayesian reconstruction (PP: 0.91). The main clade is divided into two major subclades with strong statistical support. The first subclade includes *T. camerunensis*, *T. cristatus,* and *T. montium*, but their mutual relationships remain unresolved. However, partly well supported substructure can be recognized within the two species, *T. montium* and *T. cristatus*. *Trioceros camerunensis* stands in a basal position to *T. montium*, but this is only significantly supported by the MP reconstruction. Within *T. montium*, we find a subdivision into three only slightly differentiated subclades. Overall the uncorrected *p*-distances of the included *T. montium* vouchers range between 0.00%-0.75%. Similarly, within *T. cristatus* a similar subdivision into three more distinct subclades is apparent. Here, the genetic distances between the included *T. cristatus* vouchers ranges between 0.00%–1.28%.

Contrary to the first major ingroup subclade, relationships of the species of the second major subclade remain unresolved and form a basal polytomy. Nonetheless, all terminal clades in this second major subclade are strongly supported and are well distinct regarding the individual branch lengths and bootstrap support for each terminal clade, mostly corresponding to currently accepted species within *Trioceros*. The morphologically very distinct taxon *T. eisentrauti* is grouped together with the two described *T. quadricornis* subspecies with uncorrected *p*-distance values of between 0.51%–1.08% between these three taxa. We found only one haplotype in each of the two subspecific taxa, *T. q. quadricornis* and *T. q. gracilior*, while in *T. eisentrauti* we uncovered a difference of two nucleotide substitutions in our newly gained sequences in comparison to the published 12S sequence of Pook & Wild (1997). The distances of *T. eisentrauti* to the nominate form *T. q. quadricornis* (0.51%–0.64%) are about equal in size to the distances of the latter to *T. quadricornis gracilior* (0.63%–0.64%). The distance of *T. eisentrauti* to *T. quadricornis gracilior* is only moderately higher (1.02%–1.08%). These values are clearly within the intraspecific distance range of all included *Trioceros* species. Contrarily, the remaining taxa of this subclade show a much higher genetic differentiation between each other, ranging from 3.18%–5.00%. These other terminal clades correspond to the taxa *T. pfefferi* and *T. wiedersheimi*. The latter hornless taxon is represented by three genetically well differentiated clades. Two of them correspond to the two so far described subspecies, but we find a further significant split within the populations currently assigned to the nominate form.

DISCUSSION

Following our molecular and morphological results several changes are necessary among Cameroonian chameleons of the genus *Trioceros*. The overall number of *Trioceros* taxa in Cameroon is raised to eleven and two already known taxa are revised in their taxonomic rank. Within the Cameroonian *Trioceros*, *T. oweni* is the most basal taxon, while the other taxa form two subclades, in which *T. camerunensis*, *T. cristatus, T. montium* form a lowland to submontane group while remaining taxa of the second subclade inhabit submontane to montane habitats (Pook & Wild 1997). Results and required changes will be discussed below in separate sections referring to the relevant species groups.

***Trioceros oweni* (Gray, 1831)** (Fig. 2A)

Trioceros oweni, the type species of the genus *Trioceros,* is the most basal in respect to all remaining Cameroonian taxa (Fig. 1). The value of uncorrected *p*-distance between *T. oweni* and the outgroup taxon *Kinyongia tavetana* (12.21%) is within the genetic distance range of all included *Trioceros* taxa to the outgroup (10.58–12.30%, Tab. 2, Appendix II). However, values of uncorrected *p*-distances between *T. oweni* and remaining Cameroonian *Trioceros* taxa (8.57–10.22%) are significantly higher than values in-between the remaining ingroup taxa (see Tab. 2, Appendix II), and the maximum distance value is only marginally lower than the minimum distance of all *Trioceros* to the outgroup taxon. Based on molecular data, Pook & Wild (1997) suggested that *T. oweni* might belong to a distinct species group, being closer related to *T. johnstoni*, an East African species, than to other western *Trioceros*. In the past, Werner (1902) grouped *T. oweni* together with *T. johnstoni, T. melleri* and *T. werneri*, while *T. cristatus*, *T. montium*, *T. pfefferi* and *T. quadricornis* be-

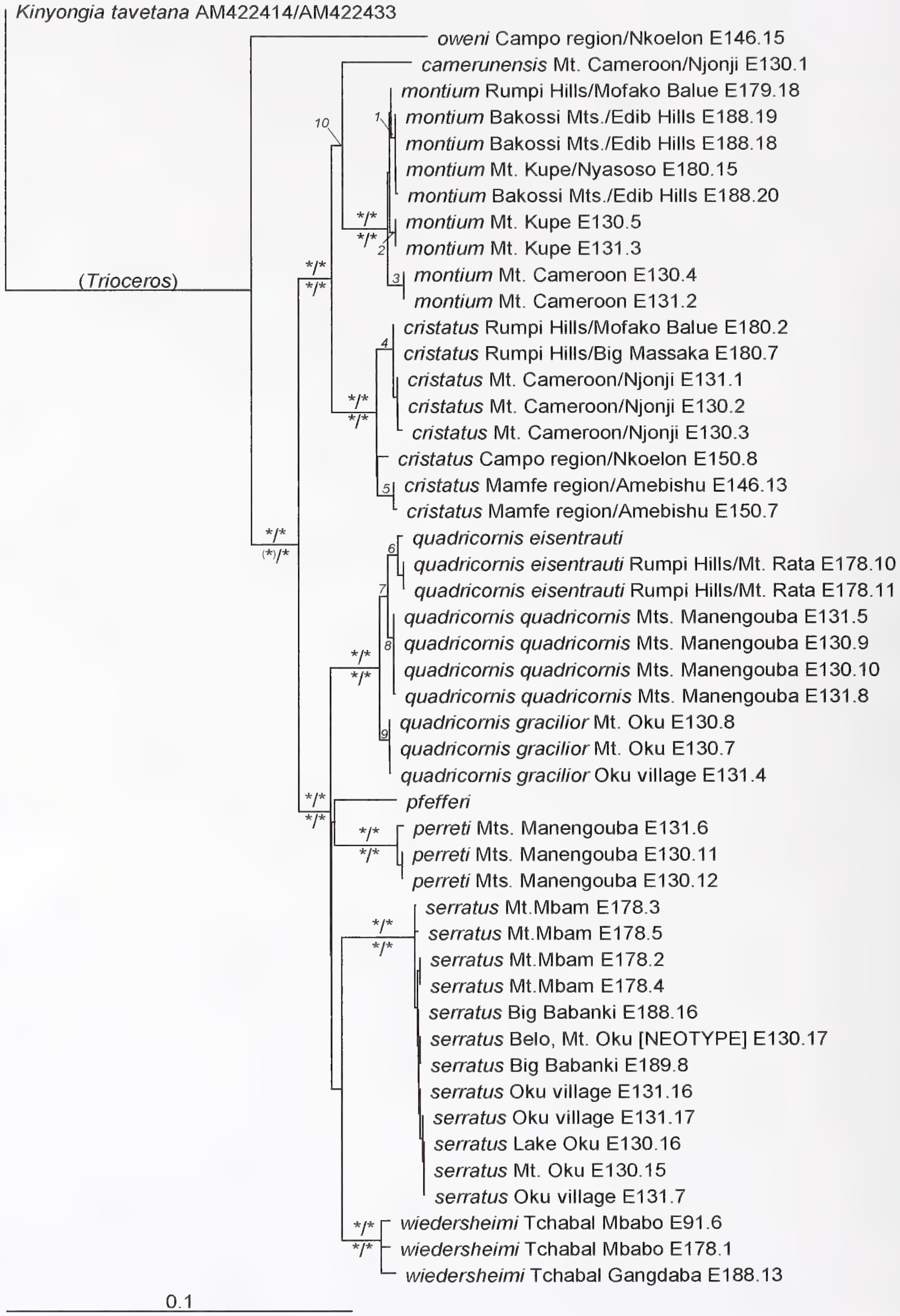
Kinyongia tavetana AM422414/AM422433
(Trioceros)
oweni Campo region/Nkoelon E146.15
camerunensis Mt. Cameroon/Njonji E130.1
montium Rumpi Hills/Mofako Balue E179.18
montium Bakossi Mts./Edib Hills E188.19
montium Bakossi Mts./Edib Hills E188.18
montium Mt. Kupe/Nyasoso E180.15
montium Bakossi Mts./Edib Hills E188.20
montium Mt. Kupe E130.5
montium Mt. Kupe E131.3
montium Mt. Cameroon E130.4
montium Mt. Cameroon E131.2
cristatus Rumpi Hills/Mofako Balue E180.2
cristatus Rumpi Hills/Big Massaka E180.7
cristatus Mt. Cameroon/Njonji E131.1
cristatus Mt. Cameroon/Njonji E130.2
cristatus Mt. Cameroon/Njonji E130.3
cristatus Campo region/Nkoelon E150.8
cristatus Mamfe region/Amebishu E146.13
cristatus Mamfe region/Amebishu E150.7
quadricornis eisentrauti
quadricornis eisentrauti Rumpi Hills/Mt. Rata E178.10
quadricornis eisentrauti Rumpi Hills/Mt. Rata E178.11
quadricornis quadricornis Mts. Manengouba E131.5
quadricornis quadricornis Mts. Manengouba E130.9
quadricornis quadricornis Mts. Manengouba E130.10
quadricornis quadricornis Mts. Manengouba E131.8
quadricornis gracilior Mt. Oku E130.8
quadricornis gracilior Mt. Oku E130.7
quadricornis gracilior Oku village E131.4
pfefferi
perreti Mts. Manengouba E131.6
perreti Mts. Manengouba E130.11
perreti Mts. Manengouba E130.12
serratus Mt.Mbam E178.3
serratus Mt.Mbam E178.5
serratus Mt.Mbam E178.2
serratus Mt.Mbam E178.4
serratus Big Babanki E188.16
serratus Belo, Mt. Oku [NEOTYPE] E130.17
serratus Big Babanki E189.8
serratus Oku village E131.16
serratus Oku village E131.17
serratus Lake Oku E130.16
serratus Mt. Oku E130.15
serratus Oku village E131.7
wiedersheimi Tchabal Mbabo E91.6
wiedersheimi Tchabal Mbabo E178.1
wiedersheimi Tchabal Gangdaba E188.13
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Fig. 1. Phylogram of the combined analysis of the 16S and 12S rRNA sequence fragments (49 sequences / 960 bp in total). The star symbol "*" denotes significantly supported nodes. [The values for the internal nodes are as follows (NJ/MP/PP/ML, respectively): 1:(78/61/0.78/73); 2:(95/98/1.00/96); 3:(99/87/0.99/99); 4:(100/98/1.00/100); 5:(100/93/1.00/100); 6:(86/96/1.00/92); 7:(81/89/0.82/86); 8:(97/67/0.56/94); 9:(100/89/0.97/99); 10:(69/83/0.61/63)].

longed to a different morphological group. A simple BLAST search in GenBank, performing a similarity check of sequences, of the applied *T. oweni*-sequence identified *T. melleri* (16S) or *T. sternfeldi* (12S) to show the highest similarity values; both again East African species. According to Townsend & Larson (2002) and Tilbury & Tolley (2009), *T. melleri* is related to *T. johnstoni*. While the only western *Trioceros* (*T. feae* from Bioko Island, Equatorial Guinea) in the study of Tilbury & Tolley (2009) is placed basal to all other *Trioceros*. Similarly, Townsend & Larson (2002) found that all western *Trioceros* (including *T. feae*) studied by them stand as a sister clade to the other members of the genus.

Hence, concerning *T. oweni* our results support the view of Pook & Wild (1997) that *Trioceros* taxa in western Central Africa are more closely related to each other than to *T. oweni*. The exact position of *T. oweni* remains to be assessed in future studies with a wider sampling from the whole distribution area of this genus.

Lowland-submontane clade

Trioceros camerunensis (Müller, 1909) (Fig. 2B)

In the past Mertens (1964) classified *T. camerunensis* as a subspecies of *T. montium* based on morphological similarities and zoogeographical affinity, but Klaver & Böhme (1992) reclassified the taxon as a valid species. Our molecular results do support close relationships between *T. camerunensis* and *T. montium* but also confirmed its full species status. According to Pook & Wild (1997), *T. camerunensis* is more closely related to *T. feae* (not included in our study) than to *T. montium*.

Lowland-submontane clade

Trioceros montium (Buchholz, 1874) (Fig. 2C)

Within the well supported monophyletic *T. montium*-clade, distinct subclades appear (Fig. 1; Tab. 2, Appendix II). Buchholz (1874) described *T. montium* from Bonjongo, Mt. Cameroon. Later Mertens (1938) described a subspecies *T. montium grafi* from Mongonge, on the opposite side of Mt. Cameroon. Klaver & Böhme (1992) regarded it only as an aberrant form and moved it in synonymy with the nominate form. Based on dorsal crest shape, Perret & Mertens (1957) indicated a possible subspecies from the Manengouba Mts. but, as in *T. m. grafi*, Klaver & Böhme (1992) proved the occurrence of this character to be more widespread. However, Pook & Wild (1997) mentioned differences in the courtship livery of *T. montium* between populations. Differences in colouration are of importance in species recognition and may play a role in character displacement (Pook & Wild 1997; Rand 1961; Wagner et al. 2009b) but further studies on this aspect are required. *Trioceros montium* inhabits the submontane zone of Mt. Cameroon, Rumpi Hills, Manengouba Mts. area and parts of the south-western edge of the Bamenda Highlands (Gonwouo et al. 2006). At first glance no morphological characters indicate a separation of populations. Hence, we refrain to draw any premature conclusions at this point.

Lowland-submontane clade

Trioceros cristatus (Stutchbury, 1837) (Fig. 2D)

A similar situation appears in *T. cristatus* and distinct subclades are detectable within this taxon and as in the preceding case, uncorrected *p*-distances show only comparatively low differences between the clades (Fig. 1; Tab. 2, Appendix II). Stutchbury (1837) described *T. cristatus* from Gabon and since then no further subspecies have been described or taxa synonymised with *T. cristatus*. *Trioceros cristatus* is widespread in the lowland to submontane zone from Nigeria to the Central African Republic, Gabon and the Republic of the Congo (Klaver & Böhme 1992; Pauwels & Vande weghe 2008). Furthermore, the species has been reported from Ghana and Togo (see references in Klaver & Böhme 1992) but, these localities must be regarded with caution, as they have not been confirmed recently. In contrast to *T. montium* the species is more widespread. A more detailed analysis of the overall distribution must be applied before any conclusions can be drawn.

Submontane-montane clade

Trioceros quadricornis (Tornier, 1899)-group (Figs 2E–G), including *Trioceros quadricornis eisentrauti* (Mertens, 1968) NEW RANK

Molecular results require changes in the former *quadricornis*-group. Morphological distinctness (body size, shape of dorsal crest, number and size of rostral horns, lung morphology) between populations from southern parts of the Cameroon mountain chain (Mt. Kupe, Manengouba Mts.) and northern parts (Bamenda Highlands to Obudu Plateau in eastern Nigeria) have already been recognized by Böhme & Klaver (1981). Uncorrected p-distance values between the taxa quadricornis and gracilior (Tab. 2, Appendix II), indicate a very recent split and these taxa correspond to subspecies. *T. q. gracilior* is known from the Bamboutos Mts, Mbulu Hills, Mt. Lefo, Mt. Oku and the Obudu Plateau, while *T. q. quadricornis* is present on Manengouba Mts. and Mt. Kupe (Böhme 1975; Böhme & Klaver 1981; Gonwouo et al. 2006; Joger 1982; Klaver & Böhme 1986, 1992).

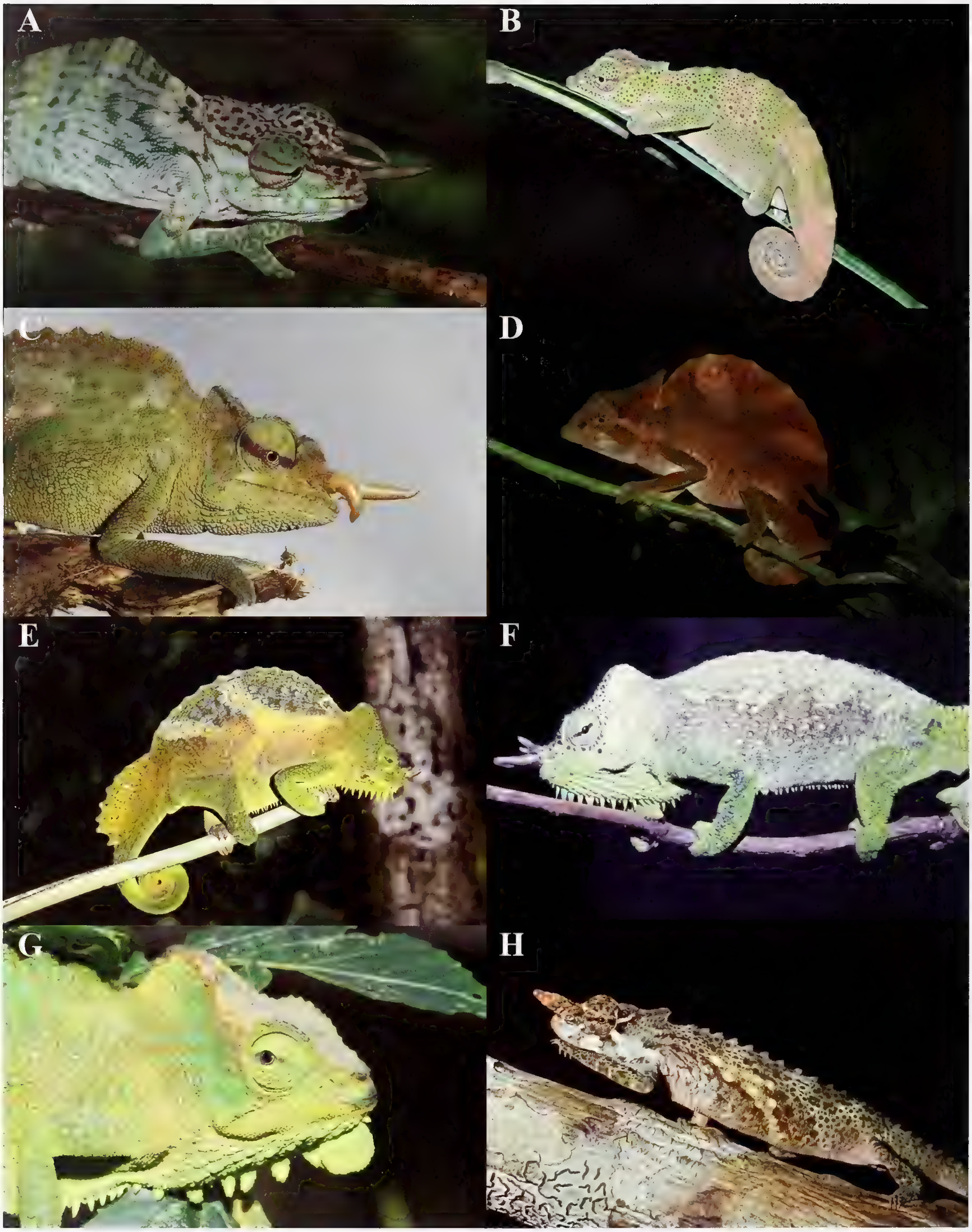

Fig. 2. Cameroonian chameleons (in life): A = *Trioceros oweni* male (Campo region; photo by J.A.M. Wurstner). B = *T. camerunensis* (Njonji, Mt. Cameroon). C = *T. montium* male; specimen with an aberrant horn shown (Big Massaka, Rumpi Hills). D = *T. cristatus* male (Nkoelon, Campo region). E = *T. q. quadricornis* male (Mt. Kupe). F = *T. q. gracilior* male (Mt. Lefo; photo by W. Böhme). G = *T. q. eisentrauti* female (Mt. Rata, Rumpi Hills). H = *T. pfefferi* male (Kodmin, Bakossi Mts.).

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We group the morphologically highly distinct taxon *T. eisentrauti* as a distinct subspecies of *T. quadricornis* (Fig. 1), a position already indicated by Pook & Wild (1997). But, while in the latter publication and in our 12S-only analysis (not shown) *eisentrauti* is placed as the basal sister taxon to the two *T. quadricornis* subspecies, according to our combined results (16S, 12S) this is not the case. Despite its morphological uniqueness (gular crest formed of flaps in *eisentrauti* and a gular crest formed of conical scales in other *Trioceros* taxa), molecular results reveal close relationships between these three taxa with values of uncorrected *p*-distances within intraspecific ranges. Values of uncorrected *p*-distances between *eisentrauti* and *T. q. quadricornis* are comparable to values between the *T. quadricornis* subspecies and values are only marginally higher between *eisentrauti* and the subspecies *T. q. gracilior* (Tab. 2, Appendix II). However, the taxa show a disjunct distribution with *T. q. quadricornis* occurring in the Manengouba area (see above) and *T. eisentrauti* being endemic to the Rumpi Hills in western Cameroon (Gonwouo et al. 2006; Klaver & Böhme 1997). All taxa inhabit pristine montane habitats, *T. q. quadricornis* occurring at altitudes between 1.800–2.250 m a.s.l., *T. q. gracilior* at altitudes between 1.800–2.400 m a.s.l. and *T. eisentrauti* in altitudes above 1.150 m a.s.l., respectively (Gonwouo et al. 2006; Pook & Wild 1997). We have located *T. eisentrauti* on Mt. Rata in the Rumpi Hills only above 1.600 m a.s.l., hence, it is probably even more restricted in its altitudinal and overall distribution range than previously indicated. In the original description of *T. eisentrauti* Mertens (1968) had already indicated relatedness to *T. quadricornis* taxa according to body size and shape of the dorsal and tail crests. Böhme & Klaver (1981) emphasized the similarities of *T. q. quadricornis* and *eisentrauti* in comparison to *T. q. gracilior* and remarked that rostral tubercles in *eisentrauti* might represent reduced rostral horns, which are present in *T. q. quadricornis* (up to two pairs of rostral horns) and *T. q. gracilior* (up to three pairs of rostral horns). However, reduction of rostral horns is also known in *T. q. quadricornis* and *T. q. gracilior* (Böhme & Klaver 1981; Mertens 1968) and Böhme & Klaver (1981) assumed that reduced horns represent a more derived character state. From the genetic point of view, we are aware that the low genetic differentiation in mitochondrial DNA might be in some cases caused by introgressive hybridization in the evolutionary history of two species. However, we believe that the similar overall morphology (body shape and size, shape of the crests) of *T. quadricornis* and *eisentrauti* also further supports our hypothesis of two closely related, but conspecific taxa. Due to the constant morphological differences between them and their allopatric distributions we regard the taxa *quadricornis* and *eisentrauti* as subspecies of a single species. *Trioceros quadricornis quadricornis* (Tornier, 1899) from the Manengouba area represents the nominate form while the taxon *eisentrauti* from the Rumpi Hills is given a new systematic status *Trioceros quadricornis eisentrauti* (Mertens, 1968) NEW RANK. In contrast to the afore discussed species (*T. montium* and *T. cristatus*), any contact zone between these two allopatric taxa can be excluded due to their highly restricted altitudinal distribution. As above, low genetic differences suggest a very recent split presumably connected to the altitudinal range shifts of the lower-temperature forests up to the mountains after the end of the Pleistocene Ice Ages (when montane forests in the tropics expanded to the lower elevations; Hewitt 2004). All three subspecific taxa of *T. quadricornis* could now represent species *in statu nascendi*.

Submontane-montane clade

Trioceros wiedersheimi (Nieden, 1910)-group (Figs 3A–G), including *Trioceros perreti* (Klaver & Böhme, 1992) NEW RANK

Further changes are necessary within the former *wiedersheimi*-group. Klaver & Böhme (1992) described the subspecies *T. w. perreti* from Manengouba Mts. Molecular results however reveal full species status for this taxon, as the uncorrected *p*-distances between *T. wiedersheimi* populations from Manengouba Mts. and populations further north (Bamenda area, Tchabal Mbabo) are clearly within the interspecific range of other western *Trioceros* species (Tab. 2, Appendix II). We thus herein elevate the taxon to the full species rank: *Trioceros perreti* (Klaver & Böhme, 1992) NEW RANK. The present distribution of *T. perreti* covers the Manengouba Mts. and the Bakossi Mts. (Euskirchen et al. 2000; Gonwouo et al. 2006).

Regarding the former nominate *T. w. wiedersheimi*, molecular and morphological results lead to recognition of two distinct clades with uncorrected *p*-values within interspecific range of this genus (Tab. 2, Appendix II). Formerly, *T. w. wiedersheimi* has been thought to occur in Cameroon north of the Manengouba Mts. (inhabited by *T. perreti* (Klaver & Böhme, 1992), see above). It has been found along the Cameroon mountain chain (Bamboutos Mts., Mbulu Hills, Mt. Lefo, Mt. Mbam, Mt. Oku and Mt. Tchabal Mbabo) and in eastern Nigeria (Gotel Mts., Mambilla Plateau and Obudu Plateau), where it inhabits montane savannas and grasslands between 1400 and 2450 m a.s.l. (Böhme & Nikolaus 1989; Chirio & LeBreton 2007; Dunger 1967; Gonwouo et al. 2006; Herrmann et al. 2006; Klaver & Böhme 1992). Nieden's (1910) description of *T. wiedersheimi* is based on two specimens, a female from Genderogebirge (=Tchabal Mbabo) and a subadult male from the village Tsch'a (Bekom), Bamenda area. In the course of describing *T. w. perreti*, Klaver & Böhme (1992) designated the female specimen as lectotype and consequently restricted the type locality to the Genderogebirge

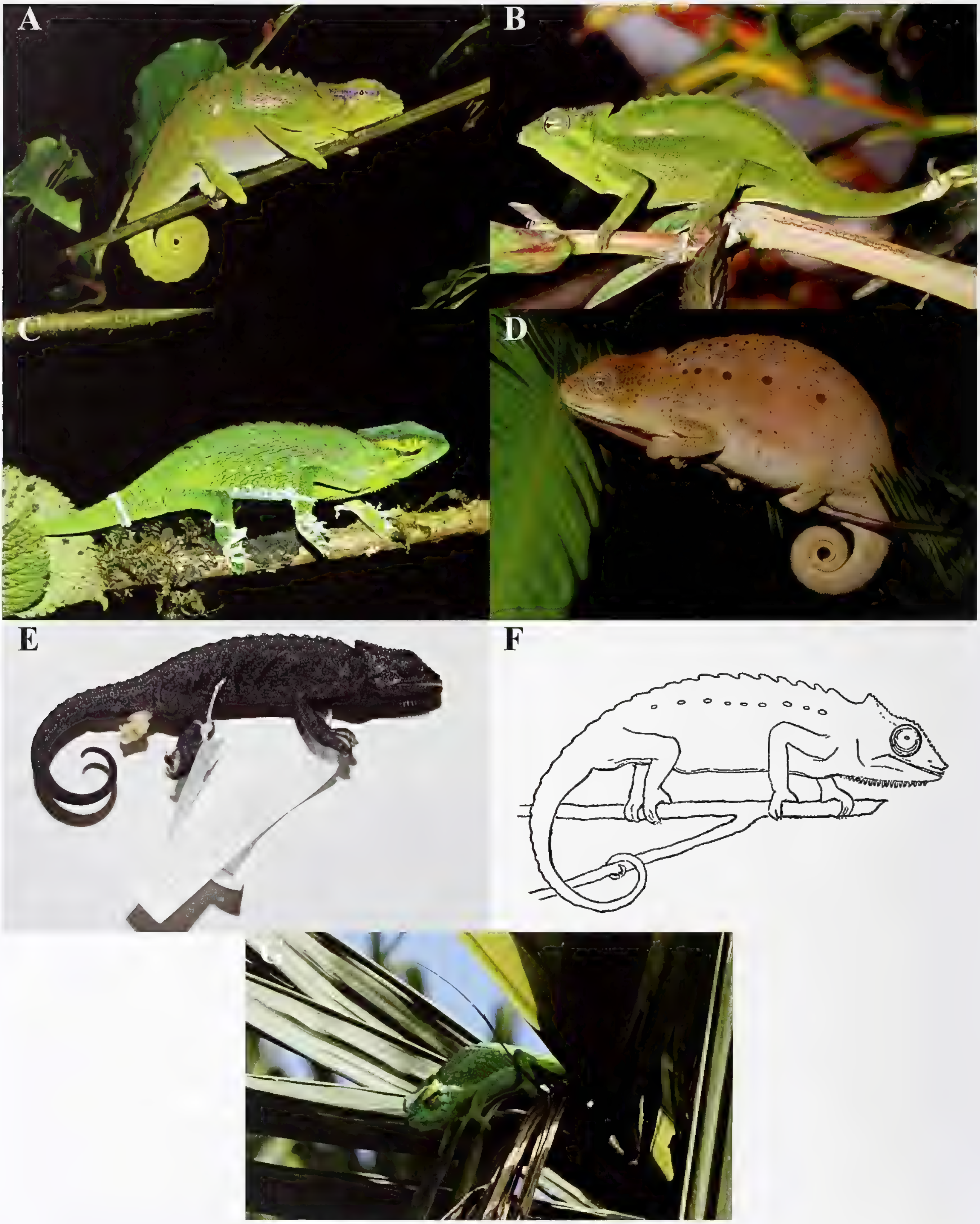

Fig. 3. Cameroonian chameleons (in life): A = *Trioceros wiedersheimi* male (Mt. Tchabal Gangdaba). B = *T. perreti* male (Kodmin, Bakossi Mts.). C = *T. serratus* male (Kedjom Keku = Big Babanki, Bamenda Highlands). D = *T. serratus* female (Kedjom Keku = Big Babanki, Bamenda Highlands). E = Male neotype of *T. serratus* (in alcohol; MNHN 2007.1494; Belo, Mt. Oku). F = Illustration of *T. serratus* after Mertens (1922; "Südkamerun"). G = Male neotype of *T. serratus* (in life; MNHN 2007.1494, Belo, Mt. Oku) in situ.

(=Tchabal Mbabo). As one of the uncovered molecular clades contains specimens from Tchabal Mbabo, topotypic material, thus this clade should correspond to *T. wiedersheimi*. The occurrence of *T. wiedersheimi* on Tchabal Gangdaba has already been assumed in the past (Chirio & LeBreton 2007; Klaver & Böhme 1992) and we can confirm its occurrence on this mountain range. Thereafter, the species is known from the northernmost parts of its former assumed distribution, while populations of the southern molecular clade from the Bamenda Highlands, Mt. Mbam, and Mt. Oku represent a distinct taxon. It is also very likely that this clade covers populations from the Mbulu Hills, Mt. Lefo and the Obudu Plateau in southern Nigeria as this would correspond to a bordering range from other studies (Gonwouo et al. 2006). Solely one locality in direct proximity north of the Manengouba Mts. (see map in Gonwouo et al. 2006) appears uncertain, as *T. perreti* has been regarded as restricted to the mountain range, but the specimen was not available to us for this study.

Mertens (1922) described *Chamaeleon serratus* from "Südkamerun" (= South Cameroon, Fig. 3F), being most similar to *T. wiedersheimi*, but differing by size, prominence of the temporal cristae and course of the lateral cristae (Fig. 3E). The species has been later synonymized with *T. wiedersheimi* by Mertens himself (1940; see below). Klaver & Böhme (1992) argued that *T. serratus* is a synonym of *T. wiedersheimi*, as the original description, especially the low number of scales on the scalloped dorsal ridge, is not consistent with *T. perreti* from Manengouba Mts. A comparison with the type specimen of *T. serratus* was not possible, as the type specimen was probably destroyed during the Second World War (H. Wermuth 16.4.1979 in litt., in Klaver & Böhme 1992).

Mertens (1922) rightly suggested that *T. wiedersheimi* is morphologically the most similar species to *T. serratus*, but obviously he only compared his material with Nieden's (1910) original description and not with the type specimen, as he only cited the original sections for comparison. Beside the characters cited above, Mertens (1922) mentioned that no additional distinct characters like the shape of the dorsal crest, which is at the origin of the specific name (Mertens 1968), are given in Nieden's (1910) description. [Remark: Nieden (1910) stated that a dorsal crest is lacking but, a dorsal midline is formed of two rows of tubercle scales which are separated in groups of 3–4 scales in the male specimen from the Bamenda region].

Later, Mertens (1940) reported on a collection delivered by M. Köhler including chameleons from the Bamenda Highlands (four males + two females) and concluded that *T. serratus* is in fact a junior synonym of *T. wiedersheimi*. His conclusion was based on the fact that males of the new material corresponded to the "paratypoid" (= paratype) of *T. serratus*, while females are consistent with the female cotype (=syntype) of *T. wiedersheimi* and finally he recognized that the prominence of the lateral and temporal cristae is subject to individual variation. In a subsequent publication on material collected by Eisentraut at Lake Oku and Lake Manengouba, Mertens (1968) confirmed his former statement and remarked that males in *T. wiedersheimi* also do possess a serrated dorsal crest, while the dorsal crest is straight and simple in females. With the exception of Lake Manengouba (recognized as distinct by Klaver & Böhme 1992), all localities of the material examined by Mertens belong to the newly discovered southern clade.

Our morphological analysis of material throughout the distribution range of the former taxon *T. w. wiedersheimi* revealed that distinguishing characters chosen by Mertens (1922) are hard to assign to members of one clade, as many characters are present in members of both clades (lack of heel spur, lack of occipital lobes, etc.) separating them from other taxa. Of the three main characters given by Mertens (1922), two of them seem to be inapplicable. According to Mertens (1922): (a) *T. serratus* grows larger than *T. wiedersheimi*, but four of ten males from Tchabal Mbabo and the Gotel Mts. (= *T. wiedersheimi*) possess a larger body length than the largest member of the southern clade, and the largest female also belongs to *T. wiedersheimi*; (b) temporal cristae are distinct in *T. wiedersheimi* and indistinct in *T. serratus*, but this character varies within both clades (Fig. 4), which was already mentioned for Bamenda populations by Mertens (1940); and (c) Mertens (1922) differentiated the course of the lateral cristae (in front of the eye first running along the eye then in a weaker slope to the tip of the snout in *T. wiedersheimi*, in contrast to an even slope in direction to the tip of the snout in *T. serratus*) and this character is clearly more applicable to specimens belonging to the southern, previously unrecognized clade (Fig. 4). Nonetheless, with just a few specimens of each clade a determination on this character alone is difficult. At last, the name-giving character, a serrated dorsal crest is also present in males of both clades. The number of scale rows forming the crenulation is consistent in both clades (being formed of up to three rows of scales) and the extent of crenulation along the dorsum and base of tail also varies in both clades. According to Mertens (1922) each cusp of the crenulation is 3 mm high and 4.5 mm long, but only in one very large specimen of *T. wiedersheimi* a comparable size has been reached, while specimens of similar size to Mertens' (1922) specimens possess smaller cusps in both clades. The given type locality "Südkamerun" does not allow any direct localization of *T. serratus*. Moreover, the subadult male paralectotype of *T. wiedersheimi* originates from the Bamenda area (part of the southern clade) and might have

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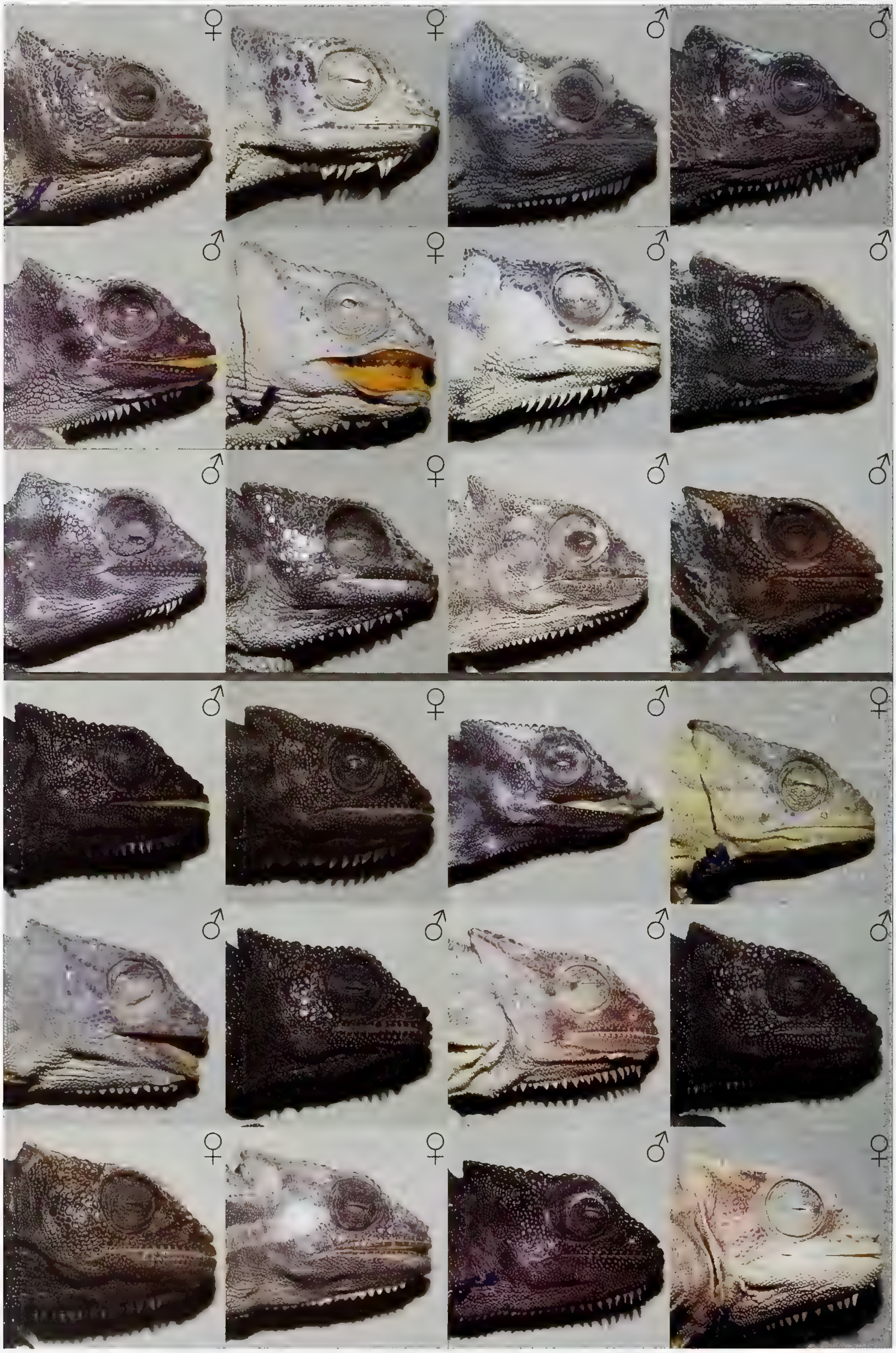

Fig. 4. Heads in lateral view. Row 1–3: *Trioceros wiedersheimi* (from left to right): ZMB 21873 female (lectotype), ZFMK 75744 female, ZFMK 68943 male, ZFMK 75740 male, ZMB 21857 male, ZMB 74805 female, ZFMK 78714 male, MNHN 2005.2753 male, NMP6V 74112 male, ZFMK 75745 female, MHNG 1544.001 male, MHNG 1544.002 male. Row 4–6: *T. serratus* (from left to right): MNHN 2007.1494 male (neotype), MNHN 2007.1465 female, NMP6V 74104 male, MHNG 1365.023 female, ZSM 13.1925 subadult male, MNHN 2007.1464 male, ZFMK 5801 male, MNHN 2007.1463 male, MNHN 2007.1461 female, MHNG 1365.024 female, MHNG 1010.049 male, ZFMK 5800 female.

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understandably mistaken as part of the distribution of *T. wiedersheimi*. The distribution of the southern clade covers the main part of former distribution of *T. wiedersheimi* and makes it more plausible to be termed "Südkamerun" (South Cameroon) in comparison to the Tchabal Mbabo area. Of Mertens (1922), most informative characters, the only reasonably useful for the recognition of *T. serratus* is the course of the lateral cristae. A course corresponding to Mertens' (1922) information is present in members of the southern clade.

According to Article 75 of the International Code of Zoological Nomenclature (ICZN 1999) a neotype is required when no name-bearing types are believed to be extant and it is necessary to define a taxon objectively. In our case, a designation of a neotype is necessary because the holotype is lost (H. Wermuth 16.IV.1979 in litt., in Klaver & Böhme 1992; A. Schlüter, herpetological curator of the SMNS, in litt. 8.III.2010) and the taxon requires unambiguous clarification of its taxonomic status. The type locality of the taxon is now set as the collecting locality of the neotype (Article 76 in ICZN 1999). Hence, we here revalidate *T. serratus* and provide a description of the neotype at the end of this section.

Submontane-montane clade

***Trioceros pfefferi* (Tornier, 1900)** (Fig. 2H)

According to Townsend & Larson (2002) *T. pfefferi* is related to (what these authors termed) *T. quadricornis* and *T. wiedersheimi*, but more closely to the latter species. While the 12S-only analysis of Pook & Wild (1997) also suggested a grouping of *T. pfefferi* and *T. wiedersheimi*, an unambiguous position of this rare taxon was not possible in our analysis with the combined 16S+12S-gene fragments (see Fig. 1). Further, because of the lack of a working 12S sequence for the sample of *T. pfefferi* that we used, we used a chimera-sequence consisting of the original 12S data as published by Pook & Wild (1997; only available in the original publication, not in GenBank) and our new 16S data of another specimen. Therefore, all that can be said for now is that *T. pfefferi* is more closely related to the taxa of the hornless *T. wiedersheimi*-complex than to *T. montium* or *T. quadricornis*, which share morphological characters like horns with *T. pfefferi*. It is also interesting to underline that the horned species, *T. montium*, *T. quadricornis* and *T. pfefferi*, do not form a monophyletic clade, and thus, horns evolved several times in the evolutionary history of the western *Trioceros* species group.

Regarding the overall distribution of *T. pfefferi*, this species shows a similar distribution pattern to two other species groups (a) *T. perreti* – *T. serratus* – *T. wiedersheimi* and (b) *T. q. quadricornis* – *T. q. gracilior*. Both groups show a rough distribution with one taxon in the Manengouba area and a second one in the Bamenda Highlands (additionally a third in the northernmost parts in the case of *T. wiedersheimi*). As in both these groups former allopatric populations have been recognized as valid taxa, the recently discovered populations of *T. pfefferi* from Mbulu Hills and Ediango (see Gonwouo et al. 2006) should be compared to southern populations in future studies, especially as the species also inhabits submontane/montane altitudes between 1100–1800 m a.s.l. and might show a disjunct distribution, as well.

Noteworthy is, that present distribution data reveal a disjunct partitioning of montane areas in the Cameroon mountain chain with related taxa (with the exception of *T. pfefferi*, but see above) but apparently the highest peak (Mt. Cameroon) does not posses an endemic montane taxon. Only the submontane *T. montium* is present on Mt. Cameroon and elevations further north, but this taxon requires further studies to understand a potential distributional separation (see above).

Designation of neotype and redescription of *Chamaeleon serratus* Mertens, 1922 (now considered as a member of the genus *Trioceros* sensu Tilbury & Tolley 2009)

Holotype (lost). *Chamaeleon serratus* Mertens (1922), Zool. Anz., 54: 191. Mus. Stuttgart, Nr. 4640 (male), probably destroyed during the Second World War (H. Wermuth 16.4.1979 in litt., in Klaver & Böhme 1992; A. Schlüter, herpetological curator of the SMNS, in litt. 8.3.2010), type locality: „Südkamerun".

Neotype. MNHN 2007.1494, adult male with everted hemipenes. Collected by Ivan Ineich on 9 May 2007 on a palm tree near road border of the road from Anyajua to Belo, close to Belo, Mt. Oku, Cameroon. Coordinates: N 06°10'32" E 10°21'09" (Lat.: 6.17547°, Lon.: 10.35244), 1339 m (4394 feet) a.s.l.

Type locality. Belo, Mt. Oku, Cameroon

Distribution. Cameroon, Nigeria

Additional material examined (Appendix I)

Diagnosis. *Trioceros serratus* differs from all other *Trioceros* except *T. wiedersheimi* and *T. perreti* by a crest formed by the canthi rostrales merging above the snout, forming a depression between the tip of the snout and the merged crest. Moreover, it can be distinguished from *T. q. eisentrauti* by the absence of gular flaps (Fig. 2D), from *T. montium*, *T. oweni*, *T. q. quadricornis*, *T. q. gracilior* and *T. pfefferi* by the absence of rostral appendages in male specimens (Figs 2A, 2C, 2E–F, 2H) and from *T. camerunensis* and *T. cristatus* by the presence of a gular crest (Figs 2B, 2D).

Trioceros serratus can be differentiated from *T. wiedersheimi* by a combination of the following characters: *T. serratus* tends to stay smaller than *T. wiedersheimi* and the tail length / body length ratio is lower in *T. serratus* (Tab. 3, Appendix II): total body length, *T. wiedersheimi* (max. total length in males: 208 mm; in females: 172 mm) growing larger than *T. serratus* (max. total length in males 179 mm; in females 158 mm), but this observation is not statistically significant (in males: $p > 0.05$ $N_{T.w.}=10$, $N_{T.s.}=27$; in females: $p > 0.05$ $N_{T.w.}=8$ $N_{T.s.}=15$); mean tail length / body length ratio is significantly higher in *T. wiedersheimi* (in males: $p < 0.05$ $N_{T.w.}=10$, $N_{T.s.}=27$; in females: $p < 0.05$ $N_{T.w.}=8$ $N_{T.s.}=15$); the mean numbers of flank scales at midbody, although values overlap, the number of flank scales at midbody is significantly higher ($p< 0.01$) in *T. serratus* (N= 44; range: 56–76, mean: 66) than in *T. wiedersheimi* (N= 19; range: 57–68, mean: 62); number of scales between the eye and the end of the head is significantly higher ($p < 0.001$) in *T. serratus* (N= 44; range: 6–11, mean: 8) than in *T. wiedersheimi* (N= 19; range: 5–9, mean: 7) and single scales tend to be distinctly larger in *T. wiedersheimi* (Fig. 4); the course of the lateral cristae in front of the eye, decreases almost steadily from the eye to the tip of the snout in *T. serratus*, while it first runs along the eye and then, from a point approximately at the middle of the eye, in a lower slope to the tip of the snout in *T. wiedersheimi*.

Trioceros serratus can be differentiated from *T. perreti* by a combination of the following characters: total body length of similar size but, although largest specimens belong to *T. serratus*, the mean total length is slightly higher in *T. perreti* (in males: $p > 0.05$ $N_{T.p.}=25$, $N_{T.s.}=27$; in females: $p > 0.05$ $N_{T.p.}=10$, $N_{T.s.}=15$); mean tail length / body length ratio is significantly higher in *T. serratus* in males ($p < 0.05$ $N_{T.p.}=25$, $N_{T.s.}=27$) lower, but not significantly, in females ($p > 0.05$ $N_{T.p.}=10$ $N_{T.s.}=15$); mean numbers of flank scales at midbody, although values clearly overlap, the number of flank scales at midbody is significantly lower ($p < 0.001$) in *T. serratus* (N= 44; range: 56–76, mean: 66) than in *T. perreti* (N= 36; range: 65–86, mean: 74; in one single specimen even 93); number of scales between the eye and the end of the head is significantly lower ($p < 0.001$) in *T. serratus* (N= 44; range: 6–11, mean: 8) than in *T. perreti* (N= 37; range: 9–15, mean: 11), scales behind the eyes are of similar size to flank scales in *T. perreti* and slightly enlarged in *T. serratus*; maximum length of gular crest is significantly higher in *T. serratus* than in *T. perreti* (in males: $p < 0.001$ $N_{T.p.}=25$, $N_{T.s.}=27$; in females: $p < 0.001$ $N_{T.p.}=12$, $N_{T.s.}=17$); length of mouth gap / distance mouth gap to tip of helmet ratio is significantly higher in males of *T. serratus* ($p < 0.05$; $N_{T.p.}=25$, $N_{T.s.}=27$), while the value is not significant in females ($p > 0.05$; $N_{T.p.}=12$, $N_{T.s.}=17$); dorsal part of the casque flat in *T. serratus* (and *T. wiedersheimi*) and convex in *T. perreti* (Böhme & Klaver 1992). For morphometrics see Tab. 3, Appendix II.

Description of the neotype. Adult male in good condition; body shape slender, laterally compressed; body length (measured from snout tip to cloaca) 83.0 mm; tail length 76.0 mm; tail base swollen and both hemipenes everted (Fig. 3F); vertical eye diameter 7.0 mm; canthus parietalis formed of 7 scales, measuring 6.8 mm (few additional slightly rough and ridged scales cranially of the parietal crest); distance snout tip to tip of helmet 24.3 mm; rostral crest merging above snout tip; rostral appendages absent; lateral and temporal crest distinct, both crests fusing posteriorly; occipital lobes absent; length of mouth gap 12.3 mm, mouth slightly opened; throat with fine longitudinal grooves between scale rows; gular crest present, formed of 24 scales, max. length of gular crest scale 1.7 mm, gular crest passing into ventral crest; lateral head scales behind eye enlarged in comparison to flank scales; lateral body scalation subhomogeneous but with interposed enlarged scales; dorsal crest present, serrated, formed out of 2–4 scales, diminishing in height caudally, scales of dorsal crest larger than flank scales; scales on extremities and tail (laterally and ventrally) of similar size as on body; fingers terminate in a single claw; hind feet without tarsal spurs.

Colouration in live (Fig. 3G): general body colouration greenish, enlarged scales on flanks pale brown, lateral and upper side of head pale bluish, upper eye border bright yellow, gular region green, upper most part of flanks and lower flank pale blue.

Colouration in alcohol (Fig. 3E): head and body dark greyish, gular crest of the same colour as body, ventral crest pale grey; sole of foot and palm of hand whitish; everted hemipenes whitish.

Variation. The number of interposed enlarged scales on flanks vary in number per line and also in number of lines. Length of gular crest scales and their number is quite variable (Tab. 3, Appendix II). Comparing the sexes, males show a higher body length – tail ratio than females and longer scales forming the gular crest (Tab. 3, Appendix II). Females generally possess a dorsal ridge, the dorsal midline is slightly serrated in one specimen (MNHN 1998.0415) forming an indistinctly serrated dorsal crest.

Colouration. The general ground coloration tends to be greenish or brownish. Enlarged scales on the flanks tend toward being brown or blue and more conspicious (Figs 3C–D). A bright stripe of differing colouration runs from the anterior part of the eye (or even starts in front of the eye) and splits into rays of colour on the eyelid; one of them running backwards along the temporal crest or between the temporal and lateral crest (Figs 3C, G). As in *T. wiedersheimi* the venter is brighter than the flanks and is pale blue or a lighter green / brown in living specimens (Fig. 3C). Blue colouration may be scattered around the mouth gap, on the top of the head, and on the flanks. The ventral line is whitish. In alcohol colourations fade away and specimens turn either pale grey-bluish (leaving some of the brighter rays on the eye visible) or turn dark and colours disappear almost completely.

Distribution. The species is known to occur in Cameroon and Nigeria. Within Cameroon it inhabits montane savannahs in the Bamenda Highlands and Mt. Mbam, and in Nigeria it has been reported from the Obudu Plateau (Böhme 1975; Akani et al. 2001). In contrast, reports from the Gotel Mts in Nigeria (Böhme & Nikolaus 1989) can be referred to *T. wiedersheimi.*

Genetics. The genetic comparison for the uncorrected *p*-distances of the combined mitochondrial 16S+12S rRNA fragments (Tab. 2, Appendix II) with the two morphologically most similar species *T. wiedersheimi* and *T. perreti* gave the following results: interspecific comparison between *T. serratus* and *T. wiedersheimi* ranged between 3.22%–4.08%, while the intraspecific variation within *T. serratus* was much lower at 0.00%–0.42% (N= 12). The interspecific difference between *T. serratus* and *T. perreti* ranges from 4.33%–4.86%, while those between the taxa *T. perreti* and *T. wiedersheimi* reach 3.74%–4.13%.

Natural history remark: Six gravid females contained the following numbers of eggs: 7, 8 (x2), 9 (x2) and 11. Size of measured eggs (N=10) ranges between 13.0–15.0 x 7.7–8.3 mm. In contrast, Angel (1940) reported ten eggs in a gravid female from the Mt. Bamboutos of 8 x 7 mm in size, which have been most probably not fully developed.

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Appendix I

List of examined specimens

***Trioceros serratus* (Mertens, 1922)**

MNHN 2007.1494 (male neotype), Cameroon, Mt. Oku, border of the road from Anyajua to Belo (near Belo, at low altitude), date 9.V.2007, coll. I. Ineich; MHNG 964.037 (male), Cameroon, Bamenda, Kishong, 1.II.1939, coll. J.-L. Perret & R. Mertens; MHNG 1010.049-50 (2 males), Cameroon, Bafoussam, Bangwa, 1959, coll. J.-L. Perret; MHNG 1365.010 (male), Cameroon, Foumban, Mt. Nkogam, III.1969, coll. J.L. Amiet; MHNG 1365.019 (male), Cameroon, Bamiléké, Foto, XI.1972, coll. J.L. Amiet; MHNG 1365.023-24 (2 females), Cameroon, Dschang, Foto, XI.1972, coll. J.L. Amiet; MNHN 1997.3642 (male), Cameroon, Oku village, V.1997, coll. L. Chirio; MNHN 1998.0415, Cameroon, Lake Oku, altitude 2200 m, 7.VI.1998, coll. L. Chirio; MNHN 1998.0416-19, Cameroon, Mt. Oku, altitude 2000-2500 m, 25.VI.1998, coll. L. Chirio; MNHN 1998.0425, MNHN 1998.0429, Cameroon, Mt. Oku, altitude 2000-2500 m, 25.VI.1998, coll. L. Chirio; MNHN 2005.2781-2787, MNHN 2005.2900 (5 males + 3 females), Cameroon, Mt. Oku, Simonkuh, 10.572°E/6.234°N, altitude 2109 m, 8.VII.2002, coll. Programme CamHerp; MNHN 2005.2788 (male), Cameroon, Oku village, 19.IV.2000, altitude 2000 m, 10.505°E/6.202°N, coll. Programme CamHerp; MNHN 2007.1461-64 (2 males + 2 females), Cameroon, Mt. Oku area, around village of Elak Oku, 6.2441°N/10.5076°E, altitude 6474 ft, 6.V.2007, coll. I. Ineich & N. Lhermitte-Vallarino; MNHN 2007.1465 (male), Cameroon, Mt. Oku area, Lake, 6.2019°N/10.4609°E, altitude 7456 ft, 8.V.2007, coll. I. Ineich & N. Lhermitte-Vallarino; NMP6V 74104 (male), Cameroon, Kedjom Keku (= Big Babanki), Bamenda Highlands, 6°06.968'N 10°15.760'E, 1290 m a.s.l., 9.XI.2009, coll. V. Gvoždík; ZFMK 5798-5801 (2 males + 2 females), Cameroon, Lake Oku, 20-30.I.1967, coll. M. Eisentraut; ZFMK 15283 (male), Cameroon, Mt. Lefo, 5.-11.X.1974, coll. W. Böhme & W. Hartwig; ZFMK 18105-6, ZFMK 18108 (male + 2 females), Cameroon, Mezam, Bafout, 1975-76, coll. P. Shu Mfosono; ZMB 21860 (female), Cameroon, Bamenda, no date; ZMB 24909 (male), Cameroon, Bamenda, coll. Adametz; ZSM 13/1925 (male), Cameroon, Tsch'a Bekom, Bamenda District, no date, coll. Glauming.

***Trioceros perreti* (Klaver & Böhme, 1992)**

MHNG 920.068-9 (male paratype + female paratype), MHNG 964.038 (female paratype), MHNG 965.054 (male paratype), MHNG 1010.052 (male holotype), MHNG 1010.053 (male paratype) Cameroon, Manengouba Mts., 1956, coll. J.-L. Perret; MHNG 1365.011 (male paratype), Cameroon, Manengouba Mts., Mwandong, 26.II.1972, coll. J.L. Amiet; MHNG 1365.012-18 (5 male paratypes + 2 female paratypes), Cameroon, Manengouba Mts., III.1973, coll. J.L. Amiet; MNHN 2007.1455-57 (3 females), Cameroon, Manengouba Mts., around Mouamena village, 9.796°E/4.984°N, altitude 4450 ft, 28.IV.2007, coll. I. Ineich & N. Lhermitte-Vallarino; MNHN 2007.1458-60 (2 males), Cameroon, Manengouba Mts., around Mouabi village, 5.0613°N/9.8155°E, altitude 5283 ft, 29.IV.2007, coll. I. Ineich & N. Lhermitte-Vallarino; MNHN 2007.1460 (male), Cameroon, Manengouba Mts., border of the road going to the lakes, 5.0512°N/9.8069°E, 28.IV.2007, coll. I. Ineich & N. Lhermitte-Vallarino; ZFMK 5802-3 (2 male paratypes), Cameroon, Manengouba Mts., Lake Manengouba, 20.XII.1966-5.I.1967, coll. M. Eisentraut; ZFMK 55599 (male), Cameroon, Manengouba, river east of Lake Manengouba, no date, F. Le Berre; ZFMK 58896-7 (2 males), Cameroon, Manengouba Mts., 1993, coll. E. Wallikewitz; ZFMK 59030 (male), Cameroon, Manengouba Mts., 1994, from pet trade; ZFMK 61836 (male), Cameroon, Manengouba area, no date, F. Le Berre; ZFMK 62571 (male), Cameroon, Manengouba area, no data, coll. unknown; ZFMK 66579 (female), Cameroon, Manengouba area, no date, from pet trade; ZFMK 66738, ZFMK 66740 (2 males), Cameroon, Manengouba area, 1998, from pet trade; ZFMK 69828, ZFMK 69830 (male + female), Cameroon, Bakossi Mts., 5.I.1998, coll. O. Euskirchen; ZFMK 69848-51 (male + 3 females), Cameroon, Bakossi Mts., 5.I.1998, coll. A. Schmitz.

***Trioceros wiedersheimi* (Nieden, 1910)**

MHNG 1544.1-2 (2 females), Cameroon, Mayo Darlé, 1941, coll. R. de Kalbermatten; MNHN 2005.2753 (female), Cameroon, Fongoi Village, Tchabal Mbabo, 12.053°E/7.230°N, altitude 1900 m, 12.I.2002, coll. Programme CamHerp; NMP6V 74112 (male), Cameroon, Tchabal Gangdaba, 7°44.678'N 12°42.741'E, 1560 m a.s.l., 26.X.2009, coll. V. Gvoždík; ZFMK 47941 (male), Nigeria, Gotel Mts. Gangirwal, app. 2400 m a.s.l., 15.II.1988, coll. G. Nikolaus; ZFMK 68943 (male), Cameroon, Tchabal Mbabo, southern slopes, XI.-5.XII.1998, coll. George & Johnson; ZFMK 75740-3 (3 males + female), Cameroon, Mayo Kelele, app. 1600 m a.s.l., 7.II.2000, coll. H.-W. Herrmann & A. Schmitz; ZFMK 75744-6 (male + 2 females), Cameroon, Tchabal Mbabo, 25.I.2001, coll. H.-W. Herrmann & A. Schmitz; ZFMK 78714 (male), Cameroon, Tchabal Mbabo, I.2001, coll. H.-W. Herrmann & A. Schmitz; ZMB 21857, ZMB 74806 (formerly part of ZMB 21857) (male + female), Cameroon, Banjo Gebirge, no date, coll. Riggenbach; ZMB 21861, ZMB 74805 (formerly part of ZMB 21861) (male + female), Cameroon, Banjo Gebirge, no date, Riggenbach; ZMB 21873 (female lectotype), Cameroon, Genderogebirge, 1500 m a.s.l., no date, coll. Riggenbach.

Appendix II

Table 1. List of voucher specimens for each species included in the present study, with their respective localities, collection numbers and GenBank accession numbers (16S, 12S) [*sequence from Pook & Wild 1997; not in GenBank; same species but different vouchers used for 16S and 12S] [**sequence from Pook & Wild 1997, not in GenBank; same voucher used for both sequences].

Species	Locality	Collection number	Accession number
Kinyongia tavetana	South Pare, Kilimanjaro, Tanzania	MHNG 2612.58	AM422414 / AM422433
Trioceros oweni [E146.15]	Nkoelon, Campo region	ZFMK 87642	HQ337816 / HQ337864
Trioceros camerunensis [E130.1]	Njonji, Mt. Cameroon	MNHN 2007.0037	HQ337798 / HQ337846
Trioceros cristatus [E130.2]	Njonji, Mt. Cameroon	MNHN 2007.1447	HQ337799 / HQ337847
Trioceros cristatus [E130.3]	Njonji, Mt. Cameroon	MNHN 2007.1448	HQ337800 / HQ337848
Trioceros cristatus [E131.1]	Njonji, Mt. Cameroon	MNHN 2007.1449	HQ337801 / HQ337849
Trioceros cristatus [E146.13]	Amebishu, Mamfe region	ZFMK 87646	HQ337802 / HQ337850
Trioceros cristatus [E150.7]	Amebishu, Mamfe region	ZFMK 87647	HQ337803 / HQ337851
Trioceros cristatus [E150.8]	Nkoelon, Campo region	ZFMK 87649	HQ337804 / HQ337852
Trioceros cristatus [E180.2]	Mofako Balue, Rumpi Hills	ZFMK 89455	HQ337805 / HQ337853
Trioceros cristatus [E180.7]	Big Massaka, Rumpi Hills	MNHG 2716.39	HQ337806 / HQ337854
Trioceros montium [E130.4]	Mt. Cameroon	MNHN 2007.1429	HQ337807 / HQ337855
Trioceros montium [E130.5]	Mt. Kupe	MNHN 2007.1445	HQ337808 / HQ337856
Trioceros montium [E131.2]	Mt. Cameroon	MNHN 2007.1430	HQ337809 / HQ337857
Trioceros montium [E131.3]	Mt. Kupe	MNHN 2007.1446	HQ337810 / HQ337858
Trioceros montium [E179.18]	Mofako Balue, Rumpi Hills	MNHG 2716.47	HQ337811 / HQ337859
Trioceros montium [E180.15]	Nyasoso, Mt. Kupe	MNHG 2716.41	HQ337812 / HQ337860
Trioceros montium [E188.18]	Edib Hills, Bakossi Mts.	NMP6V 74130/2	HQ337813 / HQ337861
Trioceros montium [E188.19]	Edib Hills, Bakossi Mts.	NMP6V 74130/1	HQ337814 / HQ337862
Trioceros montium [E188.20]	Edib Hills, Bakossi Mts.	NMP6V 74130/3	HQ337815 / HQ337863
Trioceros perreti [E130.11]	Mts. Manengouba	MNHN 2007.1458	HQ337828 / HQ337876
Trioceros perreti [E130.12]	Mts. Manengouba	MNHN 2007.1459	HQ337829 / HQ337877
Trioceros perreti [E131.6]	Mts. Manengouba	MNHN 2007.1460	HQ337830 / HQ337875
Trioceros pfefferi	Afua Ijim Forest, 10,4°E/6,15°N	MNHN 2007.1499	HQ337817 / –*
Trioceros quadricornis eisentrauti	Rumpi Hills	voucher not collected	HQ337820 / –**
Trioceros quadricornis eisentrauti [E178.10]	Mt. Rata, Rumpi Hills	ZFMK 89466	HQ337818 / HQ337866
Trioceros quadricornis eisentrauti [E178.11]	Mt. Rata, Rumpi Hills	MNHG 2716.40	HQ337819 / HQ337867
Trioceros quadricornis gracilior [E130.7]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1426	HQ337821 / HQ337868
Trioceros quadricornis gracilior [E130.8]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1423	HQ337822 / HQ337869
Trioceros quadricornis gracilior [E131.4]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1424	HQ337823 / HQ337870
Trioceros quadricornis quadricornis [E130.9]	Mts. Manengouba	MNHN 2007.1470	HQ337824 / HQ337871
Trioceros quadricornis quadricornis [E130.10]	Mts. Manengouba	MNHN 2007.1466	HQ337825 / HQ337872
Trioceros quadricornis quadricornis [E131.5]	Mts. Manengouba	MNHN 2007.1469	HQ337826 / HQ337873
Trioceros quadricornis quadricornis [E131.8]	Mts. Manengouba	MNHN 2007.1468	HQ337827 / HQ337874
Trioceros serratus [E130.15]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1463	HQ337831 / HQ337878
Trioceros serratus [E130.16]	Lake Oku, Mt. Oku, Bamenda Highlands	MNHN 2007.1465	HQ337832 / HQ337879
Trioceros serratus [E130.17] (NEOTYPE)	Belo, Mt. Oku	MNHN 2007.1494	HQ337833 / HQ337880
Trioceros serratus [E131.7]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1464	HQ337834 / HQ337881
Trioceros serratus [E131.16]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1461	HQ337835 / HQ337882
Trioceros serratus [E131.17]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1462	HQ337836 / HQ337883
Trioceros serratus [E178.2]	Mt. Mbam	voucher not collected	HQ337837 / HQ337884
Trioceros serratus [E178.3]	Mt. Mbam	voucher not collected	HQ337838 / HQ337885
Trioceros serratus [E178.4]	Mt. Mbam	voucher not collected	HQ337839 / HQ337886
Trioceros serratus [E178.5]	Mt. Mbam	voucher not collected	HQ337840 / HQ337887
Trioceros serratus [E188.16]	Big Babanki, Bamenda Highlands	NMP6V 74104	HQ337841 / HQ337888
Trioceros serratus [E189.8]	Big Babanki, Bamenda Highlands	voucher not collected	HQ337842 / HQ337889
Trioceros wiedersheimi [E91.6]	Tchabal Mbabo	ZFMK 75744	HQ337843 / HQ337890
Trioceros wiedersheimi [E178.1]	Tchabal Mbabo	voucher not collected	HQ337844 / HQ337891
Trioceros wiedersheimi [E188.13]	Tchabal Gangdaba	NMP6V 74112	HQ337845 / HQ337892

Table 2. Uncorrected *p*-distances between Cameroonian *Trioceros* taxa based on 960 bp of the 16S + 12S rRNA gene fragments.

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	*Kinyongia tavetana* AM422414/AM422433	–											
2	*oweni* Nkoelon, Campo region [E146.15]	0.1221	–										
3	*camerunensis* Mt. Cameroon [E130.1]	0.1230	0.0986	–									
4	*cristatus* Big Massaka, Rumpi Hills [E180.7]	0.1138	0.0868	0.0381	–								
5	*cristatus* Nkoelon, Campo region [E150.8]	0.1109	0.0868	0.0386	0.0086	–							
6	*cristatus* Amebishu, Mamfe region [E146.13]	0.1083	0.0857	0.0402	0.0095	0.0075	–						
7	*cristatus* Amebishu, Mamfe region [E150.7]	0.1095	0.0868	0.0412	0.0106	0.0086	0.0011	–					
8	*cristatus* Njonji, Mt. Cameroon [E130.2]	0.1151	0.0890	0.0396	0.0011	0.0096	0.0107	0.0118	–				
9	*cristatus* Njonji, Mt. Cameroon [E130.3]	0.1162	0.0901	0.0407	0.0021	0.0107	0.0118	0.0128	0.0011	–			
10	*cristatus* Njonji, Mt. Cameroon [E131.1]	0.1150	0.0879	0.0391	0.0011	0.0096	0.0105	0.0116	0.0000	0.0011	–		
11	*cristatus* Mofako Balue, Rumpi Hills [E180.2]	0.1138	0.0868	0.0381	0.0000	0.0086	0.0095	0.0106	0.0011	0.0021	0.0011	–	
12	*montium* Edib Hills, Bakossi Mts. [E188.20]	0.1159	0.0958	0.0343	0.0365	0.0326	0.0365	0.0376	0.0380	0.0391	0.0375	0.0365	–
13	*montium* Edib Hills, Bakossi Mts. [E188.18]	0.1152	0.0943	0.0338	0.0360	0.0321	0.0360	0.0370	0.0375	0.0385	0.0370	0.0360	0.0000
14	*montium* Edib Hills, Bakossi Mts. [E188.19]	0.1152	0.0943	0.0338	0.0360	0.0321	0.0360	0.0370	0.0375	0.0385	0.0370	0.0360	0.0000
15	*montium* Mt. Kupe [E130.5]	0.1153	0.0944	0.0374	0.0386	0.0332	0.0375	0.0385	0.0396	0.0407	0.0396	0.0386	0.0032
16	*montium* Mt. Kupe [E131.3]	0.1153	0.0944	0.0374	0.0386	0.0332	0.0375	0.0385	0.0396	0.0407	0.0396	0.0386	0.0032
17	*montium* Nyasoso, Mt. Kupe [E180.15]	0.1152	0.0943	0.0338	0.0360	0.0321	0.0360	0.0370	0.0375	0.0385	0.0370	0.0360	0.0000
18	*montium* Mt. Cameroon [E130.4]	0.1153	0.0964	0.0381	0.0392	0.0364	0.0402	0.0413	0.0407	0.0418	0.0402	0.0392	0.0064
19	*montium* Mt. Cameroon [E131.2]	0.1153	0.0964	0.0381	0.0392	0.0364	0.0402	0.0413	0.0407	0.0418	0.0402	0.0392	0.0064
20	*montium* Mofako Balue, Rumpi Hills [E179.18]	0.1141	0.0923	0.0349	0.0360	0.0311	0.0349	0.0360	0.0375	0.0385	0.0370	0.0360	0.0011
21	*perreti* Mts. Manengouba [E131.6]	0.1194	0.0943	0.0623	0.0528	0.0525	0.0560	0.0571	0.0545	0.0556	0.0539	0.0528	0.0591
22	*perreti* Mts. Manengouba [E130.11]	0.1227	0.0953	0.0612	0.0517	0.0514	0.0549	0.0560	0.0534	0.0545	0.0528	0.0517	0.0580
23	*perreti* Mts. Manengouba [E130.12]	0.1227	0.0953	0.0612	0.0517	0.0514	0.0549	0.0560	0.0534	0.0545	0.0528	0.0517	0.0580
24	*pfefferi*	0.1099	0.0934	0.0627	0.0603	0.0563	0.0588	0.0575	0.0616	0.0629	0.0616	0.0603	0.0538
25	*quadricornis eisentrauti* Rumpi Hills	0.1058	0.0966	0.0690	0.0639	0.0614	0.0612	0.0626	0.0652	0.0665	0.0652	0.0639	0.0611
26	*quadricornis eisentrauti* Mt. Rata, Rumpi Hills [E178.10]	0.1118	0.0948	0.0638	0.0605	0.0591	0.0606	0.0617	0.0621	0.0632	0.0616	0.0605	0.0551
27	*quadricornis eisentrauti* Mt. Rata, Rumpi Hills [E178.11]	0.1124	0.0957	0.0644	0.0611	0.0598	0.0611	0.0623	0.0629	0.0640	0.0622	0.0611	0.0556
28	*quadricornis gracilior* Mt. Oku [E130.7]	0.1117	0.0911	0.0603	0.0539	0.0525	0.0539	0.0550	0.0556	0.0567	0.0550	0.0539	0.0526
29	*quadricornis gracilior* Mt. Oku [E130.8]	0.1117	0.0911	0.0603	0.0539	0.0525	0.0539	0.0550	0.0556	0.0567	0.0550	0.0539	0.0526
30	*quadricornis gracilior* Oku village [E131.4]	0.1118	0.0922	0.0610	0.0545	0.0525	0.0545	0.0557	0.0556	0.0567	0.0556	0.0545	0.0532
31	*quadricornis quadricornis* Mts. Manengouba [E130.10]	0.1105	0.0933	0.0624	0.0560	0.0547	0.0560	0.0571	0.0577	0.0588	0.0571	0.0560	0.0548
32	*quadricornis quadricornis* Mts. Manengouba [E130.9]	0.1105	0.0933	0.0624	0.0560	0.0547	0.0560	0.0571	0.0577	0.0588	0.0571	0.0560	0.0548
33	*quadricornis quadricornis* Mts. Manengouba [E131.5]	0.1105	0.0933	0.0624	0.0560	0.0547	0.0560	0.0571	0.0577	0.0588	0.0571	0.0560	0.0548
34	*quadricornis quadricornis* Mts. Manengouba [E131.8]	0.1108	0.0944	0.0632	0.0567	0.0546	0.0567	0.0579	0.0578	0.0589	0.0578	0.0567	0.0554
35	*serratus* Belo, Mt. Oku [E130.17}	0.1174	0.1008	0.0651	0.0609	0.0601	0.0619	0.0620	0.0621	0.0632	0.0620	0.0609	0.0641
36	*serratus* Big Babanki, Bamenda Highlands [E188.16]	0.1174	0.0998	0.0646	0.0603	0.0601	0.0614	0.0615	0.0621	0.0632	0.0614	0.0603	0.0635
37	*serratus* Big Babanki, Bamenda Highlands [E189.8]	0.1180	0.1014	0.0654	0.0611	0.0609	0.0622	0.0623	0.0629	0.0640	0.0622	0.0611	0.0634
38	*serratus* Mt. Mbam [E178.2]	0.1163	0.1000	0.0664	0.0621	0.0612	0.0632	0.0633	0.0632	0.0643	0.0632	0.0621	0.0653
39	*serratus* Mt. Mbam [E178.3]	0.1165	0.0990	0.0654	0.0611	0.0602	0.0622	0.0622	0.0622	0.0633	0.0622	0.0611	0.0643
40	*serratus* Mt. Mbam [E178.4]	0.1163	0.0999	0.0664	0.0621	0.0612	0.0632	0.0632	0.0632	0.0643	0.0632	0.0621	0.0653
41	*serratus* Mt. Mbam [E178.5]	0.1151	0.0977	0.0646	0.0603	0.0601	0.0614	0.0615	0.0621	0.0632	0.0614	0.0603	0.0635
42	*serratus* Mt. Oku {E130.15]	0.1186	0.1022	0.0664	0.0621	0.0613	0.0632	0.0633	0.0632	0.0643	0.0632	0.0621	0.0654
43	*serratus* Lake Oku [E130.16]	0.1186	0.1021	0.0663	0.0621	0.0612	0.0632	0.0632	0.0632	0.0643	0.0632	0.0621	0.0653
44	*serratus* Oku village [E131.16]	0.1175	0.0998	0.0646	0.0604	0.0601	0.0614	0.0626	0.0622	0.0633	0.0615	0.0604	0.0636
45	*serratus* Oku village [E131.17]	0.1185	0.1009	0.0656	0.0614	0.0612	0.0624	0.0625	0.0632	0.0643	0.0625	0.0614	0.0646
46	*serratus* Oku village [E131.7]	0.1090	0.0988	0.0680	0.0645	0.0636	0.0633	0.0634	0.0656	0.0667	0.0656	0.0645	0.0670
47	*wiedersheimi* Tchabal Mbabo [E91.6]	0.1147	0.0923	0.0635	0.0520	0.0529	0.0533	0.0534	0.0538	0.0550	0.0531	0.0520	0.0590
48	*wiedersheimi* Tchabal Mbabo [E178.1]	0.1163	0.0900	0.0620	0.0508	0.0494	0.0498	0.0498	0.0526	0.0537	0.0519	0.0508	0.0565
49	*wiedersheimi* Tchabal Gangdaba [E188.13]	0.1146	0.0903	0.0637	0.0519	0.0527	0.0530	0.0541	0.0536	0.0547	0.0530	0.0519	0.0592

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Table 2. Continued.

	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
13	–																		
14	0.0000	–																	
15	0.0032	0.0032	–																
16	0.0032	0.0032	0.0000	–															
17	0.0000	0.0000	0.0032	0.0032	–														
18	0.0063	0.0063	0.0075	0.0075	0.0063	–													
19	0.0063	0.0063	0.0075	0.0075	0.0063	0.0000	–												
20	0.0011	0.0011	0.0021	0.0021	0.0011	0.0053	0.0053	–											
21	0.0582	0.0582	0.0578	0.0578	0.0582	0.0603	0.0603	0.0571	–										
22	0.0571	0.0571	0.0567	0.0567	0.0571	0.0592	0.0592	0.0560	0.0032	–									
23	0.0571	0.0571	0.0567	0.0567	0.0571	0.0592	0.0592	0.0560	0.0032	0.0000	–								
24	0.0535	0.0535	0.0521	0.0521	0.0535	0.0574	0.0574	0.0510	0.0365	0.0378	0.0378	–							
25	0.0599	0.0599	0.0587	0.0587	0.0599	0.0613	0.0613	0.0575	0.0370	0.0382	0.0382	0.0392	–						
26	0.0542	0.0542	0.0536	0.0536	0.0542	0.0563	0.0563	0.0522	0.0403	0.0435	0.0435	0.0368	0.0026	–					
27	0.0547	0.0547	0.0542	0.0542	0.0547	0.0568	0.0568	0.0526	0.0407	0.0439	0.0439	0.0369	0.0027	0.0000	–				
28	0.0518	0.0518	0.0513	0.0513	0.0518	0.0539	0.0539	0.0497	0.0433	0.0443	0.0443	0.0366	0.0102	0.0106	0.0107	–			
29	0.0518	0.0518	0.0513	0.0513	0.0518	0.0539	0.0539	0.0497	0.0433	0.0443	0.0443	0.0366	0.0102	0.0106	0.0107	0.0000	–		
30	0.0524	0.0524	0.0513	0.0513	0.0524	0.0545	0.0545	0.0503	0.0438	0.0448	0.0448	0.0366	0.0103	0.0107	0.0108	0.0000	0.0000	–	
31	0.0539	0.0539	0.0535	0.0535	0.0539	0.0560	0.0560	0.0518	0.0422	0.0432	0.0432	0.0367	0.0051	0.0064	0.0064	0.0063	0.0063	0.0064	–
32	0.0539	0.0539	0.0535	0.0535	0.0539	0.0560	0.0560	0.0518	0.0422	0.0432	0.0432	0.0367	0.0051	0.0064	0.0064	0.0063	0.0063	0.0064	0.0000
33	0.0539	0.0539	0.0535	0.0535	0.0539	0.0560	0.0560	0.0518	0.0422	0.0432	0.0432	0.0367	0.0051	0.0064	0.0064	0.0063	0.0063	0.0064	0.0000
34	0.0546	0.0546	0.0535	0.0535	0.0546	0.0567	0.0567	0.0525	0.0427	0.0438	0.0438	0.0367	0.0051	0.0064	0.0065	0.0064	0.0064	0.0064	0.0000
35	0.0630	0.0630	0.0622	0.0622	0.0630	0.0652	0.0652	0.0620	0.0458	0.0447	0.0447	0.0434	0.0435	0.0480	0.0487	0.0426	0.0426	0.0427	0.0437
36	0.0625	0.0625	0.0622	0.0622	0.0625	0.0646	0.0646	0.0614	0.0454	0.0444	0.0444	0.0434	0.0435	0.0478	0.0483	0.0423	0.0423	0.0428	0.0433
37	0.0634	0.0634	0.0631	0.0631	0.0634	0.0655	0.0655	0.0623	0.0461	0.0451	0.0451	0.0437	0.0442	0.0484	0.0489	0.0428	0.0428	0.0433	0.0439
38	0.0643	0.0643	0.0632	0.0632	0.0643	0.0664	0.0664	0.0632	0.0459	0.0448	0.0448	0.0434	0.0435	0.0471	0.0477	0.0416	0.0416	0.0417	0.0427
39	0.0633	0.0633	0.0622	0.0622	0.0633	0.0654	0.0654	0.0622	0.0449	0.0438	0.0438	0.0434	0.0435	0.0460	0.0467	0.0406	0.0406	0.0407	0.0417
40	0.0643	0.0643	0.0632	0.0632	0.0643	0.0664	0.0664	0.0632	0.0459	0.0448	0.0448	0.0434	0.0435	0.0471	0.0477	0.0416	0.0416	0.0417	0.0427
41	0.0625	0.0625	0.0622	0.0622	0.0625	0.0646	0.0646	0.0614	0.0444	0.0433	0.0433	0.0447	0.0448	0.0478	0.0482	0.0423	0.0423	0.0428	0.0433
42	0.0643	0.0643	0.0633	0.0633	0.0643	0.0665	0.0665	0.0633	0.0470	0.0460	0.0460	0.0447	0.0447	0.0493	0.0500	0.0438	0.0438	0.0439	0.0449
43	0.0643	0.0643	0.0632	0.0632	0.0643	0.0664	0.0664	0.0632	0.0470	0.0459	0.0459	0.0447	0.0447	0.0492	0.0499	0.0438	0.0438	0.0438	0.0449
44	0.0626	0.0626	0.0623	0.0623	0.0626	0.0647	0.0647	0.0615	0.0455	0.0444	0.0444	0.0446	0.0434	0.0479	0.0483	0.0423	0.0423	0.0428	0.0434
45	0.0636	0.0636	0.0633	0.0633	0.0636	0.0657	0.0657	0.0625	0.0465	0.0454	0.0454	0.0447	0.0447	0.0488	0.0493	0.0433	0.0433	0.0439	0.0444
46	0.0658	0.0658	0.0648	0.0648	0.0658	0.0669	0.0669	0.0647	0.0486	0.0475	0.0475	0.0447	0.0447	0.0475	0.0483	0.0419	0.0419	0.0419	0.0429
47	0.0591	0.0591	0.0587	0.0587	0.0591	0.0612	0.0612	0.0568	0.0374	0.0363	0.0363	0.0337	0.0318	0.0342	0.0345	0.0329	0.0329	0.0333	0.0329
48	0.0565	0.0565	0.0562	0.0562	0.0565	0.0609	0.0609	0.0543	0.0388	0.0377	0.0377	0.0340	0.0321	0.0345	0.0348	0.0333	0.0333	0.0337	0.0332
49	0.0583	0.0583	0.0580	0.0580	0.0583	0.0604	0.0604	0.0562	0.0413	0.0403	0.0403	0.0389	0.0341	0.0352	0.0354	0.0350	0.0350	0.0354	0.0360

	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
32	–																	
33	0.0000	–																
34	0.0000	0.0000	–															
35	0.0437	0.0437	0.0438	–														
36	0.0433	0.0433	0.0439	0.0000	–													
37	0.0439	0.0439	0.0445	0.0000	0.0000	–												
38	0.0427	0.0427	0.0428	0.0011	0.0011	0.0011	–											
39	0.0417	0.0417	0.0417	0.0011	0.0011	0.0011	0.0000	–										
40	0.0427	0.0427	0.0428	0.0011	0.0011	0.0011	0.0000	0.0000	–									
41	0.0433	0.0433	0.0439	0.0021	0.0021	0.0021	0.0011	0.0011	0.0011	–								
42	0.0449	0.0449	0.0450	0.0011	0.0011	0.0011	0.0021	0.0021	0.0021	0.0032	–							
43	0.0449	0.0449	0.0449	0.0011	0.0011	0.0011	0.0021	0.0021	0.0021	0.0032	0.0000	–						
44	0.0434	0.0434	0.0439	0.0021	0.0021	0.0022	0.0032	0.0032	0.0032	0.0042	0.0011	0.0011	–					
45	0.0444	0.0444	0.0449	0.0011	0.0011	0.0011	0.0021	0.0022	0.0021	0.0032	0.0000	0.0000	0.0011	–				
46	0.0429	0.0429	0.0430	0.0011	0.0011	0.0012	0.0023	0.0023	0.0023	0.0034	0.0000	0.0000	0.0011	0.0000	–			
47	0.0329	0.0329	0.0334	0.0344	0.0341	0.0340	0.0333	0.0322	0.0333	0.0341	0.0357	0.0356	0.0352	0.0352	0.0378	–		
48	0.0332	0.0332	0.0337	0.0369	0.0365	0.0365	0.0359	0.0348	0.0359	0.0365	0.0382	0.0381	0.0377	0.0376	0.0403	0.0045	–	
49	0.0360	0.0360	0.0365	0.0375	0.0371	0.0377	0.0365	0.0355	0.0365	0.0371	0.0387	0.0386	0.0372	0.0382	0.0408	0.0068	0.0066	–

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Table 3. Summary of morphological measures (mm) of adult male and female *Trioceros perreti, T. wiedersheimi* and *T. serratus*. Given are sample size (N), minimum (min), maximum (max), mean values (mean) and standard deviation (s.dev.) GC = number of scales forming gular crest, BL = body length from tip of snout to cloaca, TL = tail length from cloaca to tip of tail, ED = vertical eye diameter, StHt = distance snout tip to tip of helmet, HW = head width, MG = mouth gap, MGHt = distance mouth gap to tip of helmet, TiL = tibia length, FoL = fore arm length, GL = length of gular crest, SHE = number of scale between eye and end of head, FSM = flank scales at midbody, TL/BL = tail length / body length ratio, TiL/BL = tibia length / body length ratio, FoL/BL forearm length / body length ratio, MG/StHt = mouth gap / snout tip to tip of helmet ratio, HW/StHt = head width / snout tip to tip of helmet ratio, ED/MG = eye diameter /mouth gap ratio, ED/HW = eye diameter / head width ratio, MG/MGHt = mouth gap / mouth gap to tip of helmet ratio.

	GC	BL	TL	ED	StHt	HW	MG	MGHt	TiL	FoL	GL	SHE	FSM	TL/BL	TiL/BL	FoL/BL	MG/StHt	HW/StHt	ED/MG	ED/HW	ED/MG	G/MGHt
***Trioceros perreti* (males)**																						
N	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
min	11	63.0	53.0	6.1	21.0	6.5	10.3	14.4	10.1	11.1	0.5	9	65	0.72	0.14	0.15	0.47	0.28	0.54	0.94	0.54	0.68
max	37	81.0	74.0	8.0	26.0	9.7	13.6	17.7	14.2	15.3	1.3	15	93	1.04	0.18	0.20	0.55	0.38	0.63	1.25	0.63	0.82
mean	21.4	74.2	64.6	6.9	23.1	7.6	11.8	16.0	12.0	12.8	0.9	11	75	0.87	0.16	0.17	0.51	0.33	0.58	1.12	0.58	0.73
s.dev.	6	4.4	5.9	0.5	1.4	0.7	0.8	1.0	0.9	1.0	0.2	1.7	6.6	0.08	0.01	0.01	0.02	0.02	0.02	0.07	0.02	0.04
***Trioceros wiedersheimi* (males)**																						
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
min	14	61.0	60.5	5.8	19.7	6.4	9.9	13.4	10.6	11.0	1.4	5	57	0.89	0.15	0.16	0.47	0.32	0.57	1.03	0.57	0.69
max	23	100.5	107.5	8.2	26.3	9.1	13.1	18.1	16.7	17.6	2.2	8	64	1.10	0.18	0.19	0.53	0.36	0.64	1.23	0.64	0.83
mean	18.2	80.4	82.6	7.0	22.8	7.9	11.5	15.7	13.5	14.3	1.8	7	61	1.02	0.17	0.18	0.50	0.35	0.61	1.14	0.61	0.74
s.dev.	3	13.4	17.9	0.9	2.2	0.8	1.3	1.6	2.0	2.3	0.3	1.2	2.1	0.07	0.01	0.01	0.02	0.02	0.02	0.07	0.02	0.04
***Trioceros serratus* (males)**																						
N	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27
min	15	52.0	46.5	5.4	17.0	6.0	8.3	11.6	8.2	8.4	0.8	6	56	0.83	0.15	0.15	0.47	0.30	0.55	1.04	0.55	0.68
max	29	88.0	91.0	8.1	25.2	10.3	13.3	17	14.4	15.0	2.7	10	76	1.03	0.17	0.18	0.55	0.43	0.65	1.34	0.65	0.86
mean	21.9	74.9	69.0	6.7	22.3	8.0	11.5	15	12.1	12.6	1.6	8	65	0.92	0.16	0.17	0.51	0.36	0.59	1.19	0.59	0.76
s.dev.	4	8.5	9.4	0.7	2.2	1.0	1.3	1	1.4	1.5	0.4	1.2	5.4	0.06	0.01	0.01	0.02	0.03	0.02	0.06	0.02	0.04
***Trioceros perreti* (females)**																						
N	12	12	10	12	12	12	12	12	12	12	12	12	12	10	12	12	12	12	12	12	12	12
min	12	70.0	54.0	6.2	21.7	6.7	11.1	14.4	11.5	11.6	0.6	9	67	0.75	0.15	0.15	0.49	0.28	0.53	1.00	0.53	0.72
max	30	95.0	67.0	7.5	27.2	8.5	13.5	18.2	14.6	15.1	1.0	12	83	0.90	0.18	0.19	0.54	0.34	0.58	1.22	0.58	0.82
mean	20.5	78.3	62.0	6.7	23.4	7.5	12.1	15.9	12.8	13.3	0.8	11	73	0.81	0.16	0.17	0.51	0.32	0.56	11.18	0.56	0.76
s.dev.	7	7.4	3.6	0.4	1.4	0.5	0.7	1.1	0.9	1.1	0.1	1.0	5.2	0.05	0.01	0.01	0.02	0.02	0.01	0.06	0.01	0.03
***Trioceros wiedersheimi* (females)**																						
N	9	9	8	9	9	9	9	9	9	9	9	9	9	8	9	9	9	9	9	9	9	9
min	15	68.0	52.0	6.3	20.5	6.6	10.4	13.7	11.6	12.0	1.0	5	57	0.76	0.16	0.16	0.48	0.30	0.55	0.97	0.55	0.71
max	23	87.0	86.0	7.7	25.4	8.4	13.3	16.3	13.9	15.0	2.5	9	68	1.00	0.17	0.18	0.53	0.36	0.61	1.21	0.61	0.84
mean	19.4	78.9	67.0	6.9	22.9	7.4	11.8	15.2	12.9	13.5	1.5	7	63	0.86	0.16	0.17	0.52	0.33	0.58	1.09	0.58	0.78
s.dev.	3	6.7	9.8	0.5	1.7	0.5	1.0	0.9	0.8	1.1	0.5	1.1	3.4	0.08	0.01	0.01	0.02	0.02	0.02	0.08	0.02	0.05
***Trioceros serratus* (females)**																						
N	17	17	15	17	17	17	17	17	17	17	17	17	17	15	17	17	17	17	17	17	17	17
min	19	55.0	45.0	5.5	18.1	5.5	8.8	12.0	8.5	9.0	0.6	6	60	0.63	0.15	0.14	0.47	0.29	0.52	1.01	0.52	0.70
max	31	92.0	70.0	7.5	24.8	9.3	13.4	16.8	14.5	14.9	1.9	11	76	0.86	0.18	0.18	0.58	0.38	0.63	1.27	0.63	0.87
mean	23.1	74.6	57.4	6.5	21.7	7.3	11.4	14.4	11.9	12.3	1.3	8	67	0.77	0.16	0.16	0.52	0.34	0.57	1.12	0.57	0.79
s.dev.	3	10.3	7.2	0.7	2.1	1.1	1.5	1.4	1.7	1.8	0.4	1.2	4.4	0.06	0.01	0.01	0.03	0.03	0.03	0.08	0.03	0.05

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Another new *Cophixalus* species (Amphibia: Anura: Microhylidae) from western New Guinea

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Abstract. Based on external morphological, anatomical, bioacoustic, and molecular traits, a new species in the microhylid genus *Cophixalus* is described. The new species was discovered in the Fakfak Mountains, northwestern corner of the Bomberai Peninsula, Papua Province, Indonesia. The new taxon is most closely related to the sympatric *Cophixalus tetzlaffi*. It differs from that species in several morphological traits, but primarily by its advertisement call: the new species utters a single peeping note with a mean duration of less than 200 milliseconds, whereas the advertisement call of *C. tetzlaffi* consists of three to four notes, with a mean note duration of more than 400 milliseconds. Molecular data (mitochondrial 16S rRNA) support the determination of the specific distinctness of the new species.

Key words. Anura, Asterophryinae, *Cophixalus*, new species, New Guinea.

INTRODUCTION

Fifty-one species in the microhylid frog genus *Cophixalus* are known at present (Frost 2010). Of these, 14 occur in north-eastern Australia, 30 in Papua New Guinea, three are known only from the Papua Province of Indonesia, three are recorded from both Papua New Guinea and the Papua Province of Indonesia, and one species seems to be endemic to the Island of Halmahera, located about 300 km west of the western tip of New Guinea. Although many new *Cophixalus* species are expected to be described also from western New Guinea, the distribution centre of the genus seems to be clearly in eastern New Guinea and north-eastern Australia. *Cophixalus montanus* has been known since 1895 from Halmahera, and the detection of three new species in the western part of New Guinea (on Yapen Island, on the Wandammen Peninsula, and on the Bomberai Peninsula) came as a surprise (Günther 2003, 2006).

Here I describe another new species from the Fakfak Mountains on the Bomberai Peninsula (located on the "throat" of the Vogelkop) found during an expedition in September 2008. Moreover, a population of *Cophixalus tridactylus* and one specimen of a second undescribed species was observed there. Consequently, at least four *Cophixalus* species occur syntopically in the middle and higher elevations (400–1000 m above sea level, a.s.l.) of the Fakfak Mountains.

MATERIAL AND METHODS

Most frogs were collected at night after locating them by their advertisement calls. Some specimens were photographed in life the next day and all specimens were anaesthetized with chlorobutanol and subsequently fixed in 2 % formalin. Tissue probes from thigh muscle were taken from some frogs and stored in about 96 % ethanol to enable DNA sequencing, before fixing the animals in formalin. All specimens were transferred to 75 % ethanol later in the Berlin museum. One specimen was cleared and stained as an osteological preparation according to a method modified from Dingerkus & Uhler (1977).

The following measurements were taken with a digital calliper (> 10 mm) or with a binocular dissecting microscope fitted with an ocular micrometer (< 10 mm) to the nearest 0.1 mm:

SUL – snout-urostyle length: from tip of snout to distal tip of urostyle-bone; SUL is about one to two mm shorter than the snout-vent length (SVL). As the measurement error is higher in the latter, I prefer to use the former. In general, both measurements are more or less identical and are used interchangeably in this paper.
TL – tibia length: external distance between knee and ankle;
TaL – length of tarsus: external distance, tarsal and ankle joints held at a right angle;

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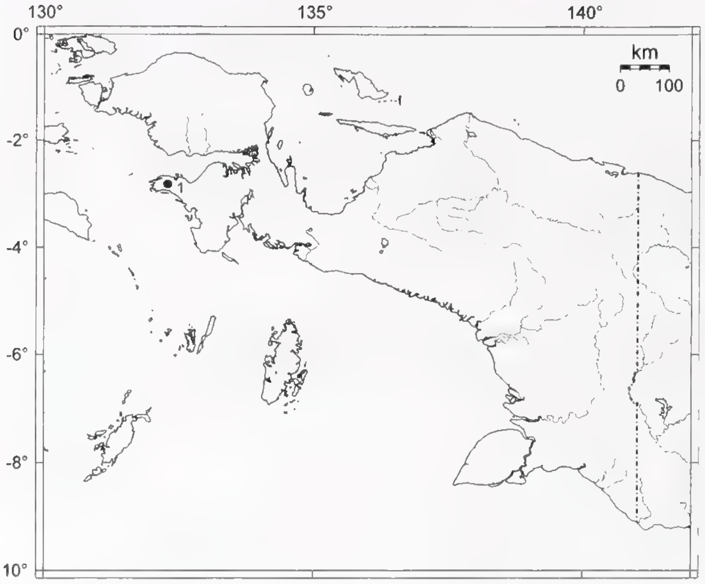

Fig. 1. Map of the western part of New Guinea with type locality (1).

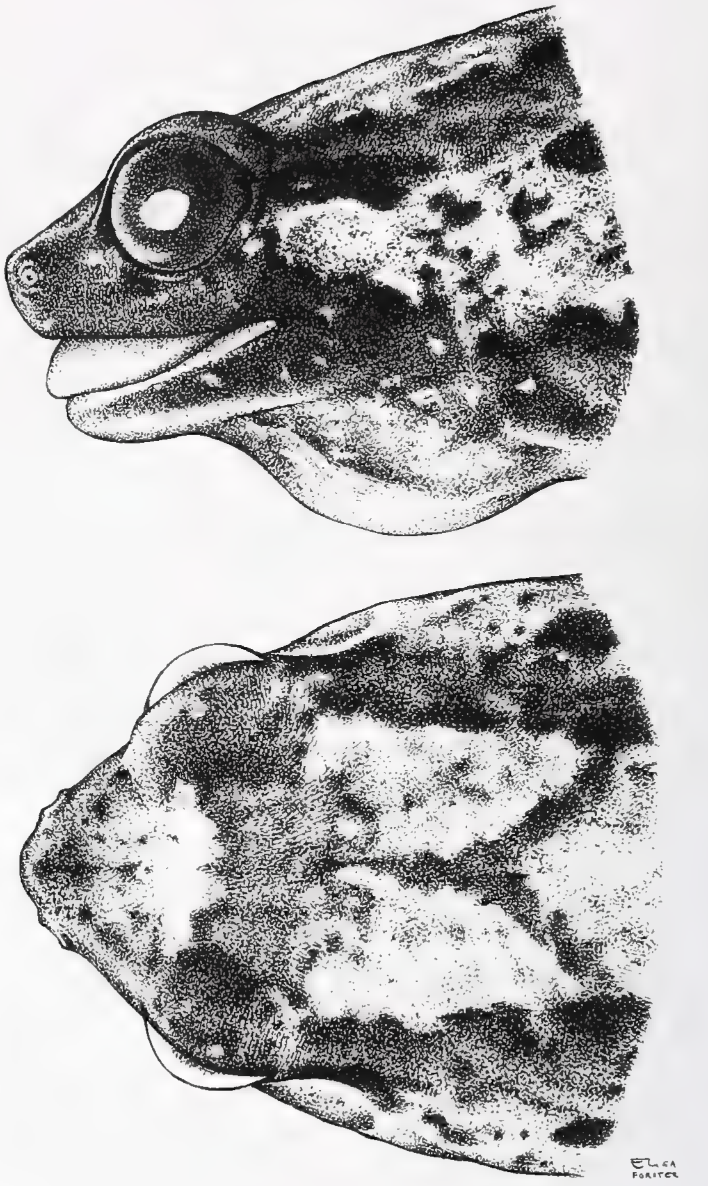

Fig. 2. Holotype of *Cophixalus monosyllabus* sp. n. head in lateral view (above); head in dorsal view (below).

T4L – length of fourth toe: from tip of toe to proximal end of inner metatarsal tubercle;
T4D – transverse diameter of disc of fourth toe;
F3L – length of third toe;
F3D – transverse diameter of disc of third finger;
F1D – transverse diameter of disc of first finger;
T1D – transverse diameter of disc of first toe;
HL – head length: from tip of snout to posterior margin of tympanum;
HW – head width, taken in the region of the tympana;
SL – snout length: from an imaginary line that connects the centres of eyes to tip of snout;
END – distance from anterior corner of orbital opening to centre of naris;
IND – internarial distance between centres of nares;
ED – eye diameter: from anterior to posterior corner of orbital opening;
TyD – horizontal diameter of tympanum.

Advertisement calls were recorded under natural conditions with a Sony Digital Audio Tape (DAT) Walkman TCD-D 100 and a Sennheiser microphone MKE 300 and analysed with Avisoft-SAS Lab Pro software. All specimens are currently stored in the Museum für Naturkunde Berlin (ZMB) and bear registration numbers of that institution. Part of the type series will later be transferred to the Museum Zoologicum Bogoriense (MZB).

RESULTS AND DISCUSSION

Cophixalus monosyllabus sp. n.

Holotype. ZMB 74993 (field number, FN: RG 7888) ; adult male collected by R. Günther and A. Piahar 6 km direct line NNE of Fakfak town, near the Fakfak-Kokas road, Bomberai Peninsula (neck of Vogelkop), Papua Province, Indonesia, 2°53'S and 132°18'E, elevation 500 m a.s.l., 9 September 2008 (Fig. 1).

Paratypes. ZMB 74994 (FN: RG 7889), ZMB 74995 (FN: RG 7890), ZMB 74996 (FN: RG 7912), ZMB 74997 (FN: RG 7915), ZMB 74998 (FN: RG 7916), ZMB 74999 (FN: RG 7926), ZMB 75000 (FN: RG 7927), ZMB 75001 (FN: RG 7951), ZMB 75002 (FN: RG 7952). ZMB 74997 is now an osteological preparation. All nine paratypes are males. They were collected from 9 to 14 September 2008 along the Fakfak-Kokas road in the southern part of the Fakfak Mountains, at elevations of from 400 to 700 m a.s.l. Collectors were R. Günther, M. Kapisa, and A. and F. Piahar.

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Table 1. Body measurements and body ratios of the type series of *Cophixalus monosyllabus* sp. n. ZMB-No are the inventory numbers of the Museum für Naturkunde Berlin, FN are the field numbers of the author, SD indicates the standard deviation. ZMB 74993 is the holotype; ZMB 74997 is now an osteological preparation. All specimens are adult males. All measurements are in mm; abbreviations are explained in "Material and methods".

ZMB-No	74993	74994	74995	74996	74997	74998	74999	75000	75001	75002	mean	SD
FN	7888	7889	7890	7912	7915	7916	7926	7927	7951	7952	22.9	1.04
SUL	22.8	23.1	24.1	22.5	22.4	23.6	20.6	22.8	24.3	23.0		
TL	10.9	11.7	11.4	11.5	11.3	11.5	10.1	11.7	12.3	11.7		
TaL	7.4	7.2	7.1	6.8	6.9	7.2	7.2	7.6	7.3	7.3		
T4L	11.5	11.6	11.7	11.6	11.2	11.1	10.5	11.1	12.5	10.9		
T4D	1.3	1.25	1.4	1.0	1.3	1.3	1.0	1.2	1.35	1.25		
T1D	0.7	0.65	0.75	0.5	0.7	0.6	0.45	0.7	0.6	0.6		
F3L	6.0	6.4	6.8	6.4	6.1	6.5	5.5	5.9	6.8	6.0		
F3D	1.4	1.4	1.7	1.45	1.5	1.3	1.25	1.5	1.5	1.4		
F1D	0.6	0.45	0.50	0.50	0.5	0.4	0.45	0.5	0.5	0.5		
HL	7.5	7.2	8.2	7.1	7.3	8.0	6.8	7.3	7.5	7.5		
HW	8.5	9.0	9.1	9.0	9.5	9.8	8.5	9.0	9.6	9.6		
SL	3.2	3.3	3.6	3.3	3.5	3.4	3.2	3.3	3.5	3.6		
END	2.2	2.1	2.5	2.0	2.1	2.2	2.0	2.1	2.2	2.0		
IND	2.3	2.5	2.5	2.3	2.2	2.4	2.2	2.5	2.5	2.25		
ED	2.8	2.9	3.1	2.5	2.9	2.8	2.7	2.8	3.0	3.0		
TyD	1.2	1.0	1.2	1.0	1.0	1.1	1.0	0.9	1.0	1.0		
TL/SUL	0.48	0.51	0.47	0.51	0.50	0.49	0.49	0.51	0.51	0.51	0.50	0.051
TaL/SUL	0.32	0.31	0.29	0.30	0.31	0.31	0.35	0.33	0.30	0.32	0.31	0.017
T4L/SUL	0.50	0.50	0.49	0.52	0.50	0.47	0.51	0.49	0.51	0.47	0.50	0.016
F3L/SUL	0.26	0.28	0.28	0.28	0.27	0.28	0.27	0.26	0.28	0.26	0.27	0.009
F3D/SUL	0.061	0.060	0.071	0.064	0.067	0.055	0.061	0.066	0.062	0.061	0.063	0.004
F1D/SUL	0.026	0.019	0.021	0.022	0.031	0.017	0.022	0.022	0.021	0.022	0.021	0.002
T4D/SUL	0.057	0.054	0.058	0.044	0.058	0.055	0.049	0.053	0.056	0.054	0.054	0.004
T1D/SUL	0.031	0.028	0.031	0.022	0.031	0.025	0.022	0.031	0.025	0.026	0.027	0.004
HL/SUL	0.33	0.31	0.34	0.32	0.33	0.34	0.33	0.32	0.31	0.33	0.33	0.011
HW/SUL	0.37	0.39	0.38	0.40	0.42	0.42	0.41	0.39	0.40	0.42	0.40	0.018
HL/HW	0.88	0.80	0.90	0.79	0.77	0.82	0.80	0.81	0.78	0.78	0.81	0.043
END/IND	0.96	0.84	0.84	0.87	0.95	0.92	0.91	0.84	0.88	0.89	0.89	0.044
ED/SUL	0.123	0.125	0.129	0.111	0.129	0.119	0.131	0.123	0.120	0.130	0.124	0.006
TyD/ED	0.43	0.34	0.39	0.40	0.34	0.39	0.37	0.32	0.33	0.33	0.36	0.037
SL/SUL	0.140	0.143	0.149	0.147	0.156	0.144	0.155	0.145	0.141	0.156	0.148	0.006

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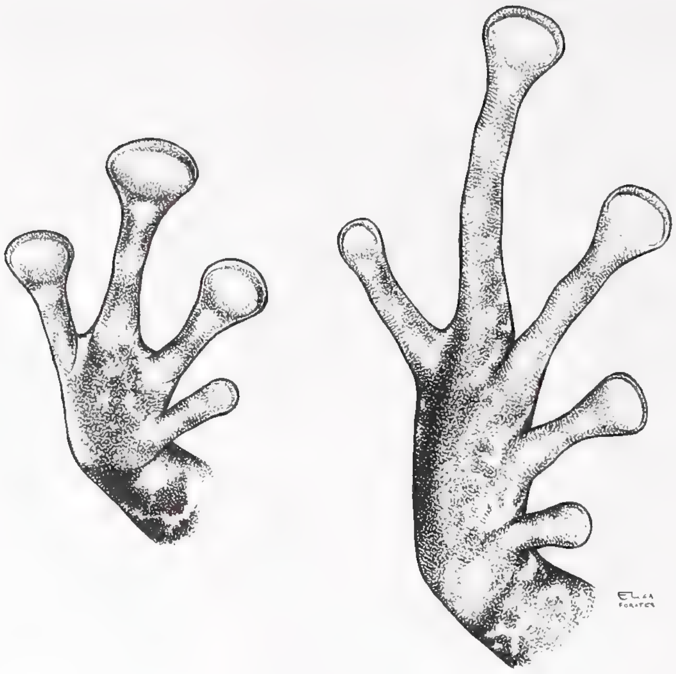

Fig. 3. Holotype of *Cophixalus monosyllabus* sp. n. ventral view of right hand (left); ventral view of right foot (right).

Diagnosis. With a snout-urostyle length of from 20.6 to 24.3 mm in ten adult males, the new species belongs to the middle-sized species of the genus. It is obviously a sister species of the sympatric *Cophixalus tetzlaffi* and differs from all other species in the same characters as the latter. The new species differs from *C. tetzlaffi,* among others, by its larger body size, its wider finger and toe discs, and its advertisement call which consists of only one peeping syllable (note) that lasts, on average, 196 milliseconds (ms). In contrast, the advertisement call of *C. tetzlaffi* consists of three to four peeping notes, with a mean note length of more than 400 ms.

Description of the holotype. For measurements see Table 1. Head broader than long (HL/HW ratio 0.88), canthus rostralis roundish; loreal region straight; snout slightly protruding in profile (Fig. 2, above) and rounded in dorsal view (Fig. 2, below); horizontal eye diameter greater than eye-naris distance; borders of tympanum scarcely visible, its size less than half of the eye diameter (TyD/ED 0.43), no supratympanic fold; internarial distance slightly greater than distance between eye and naris (END/IND 0.96); tongue large, posteriorly broadened and without posterior notch, its posterior and lateral margins free; a strongly serrated fold present in front of the pharynx; long

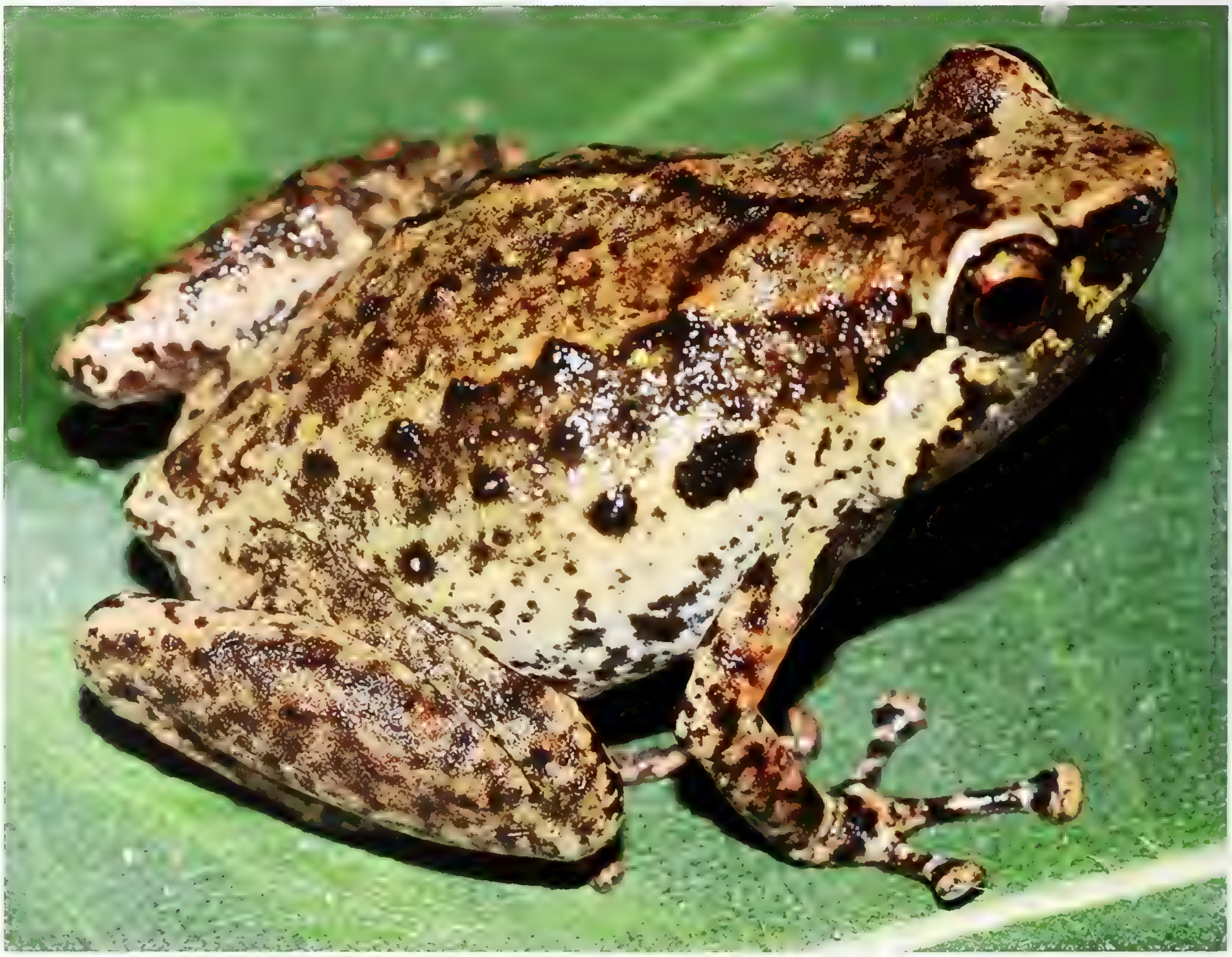

Fig. 4. Dorsolateral view of a more brownish coloured paratype of *Cophixalus monosyllabus* sp. n. (ZMB 74995).

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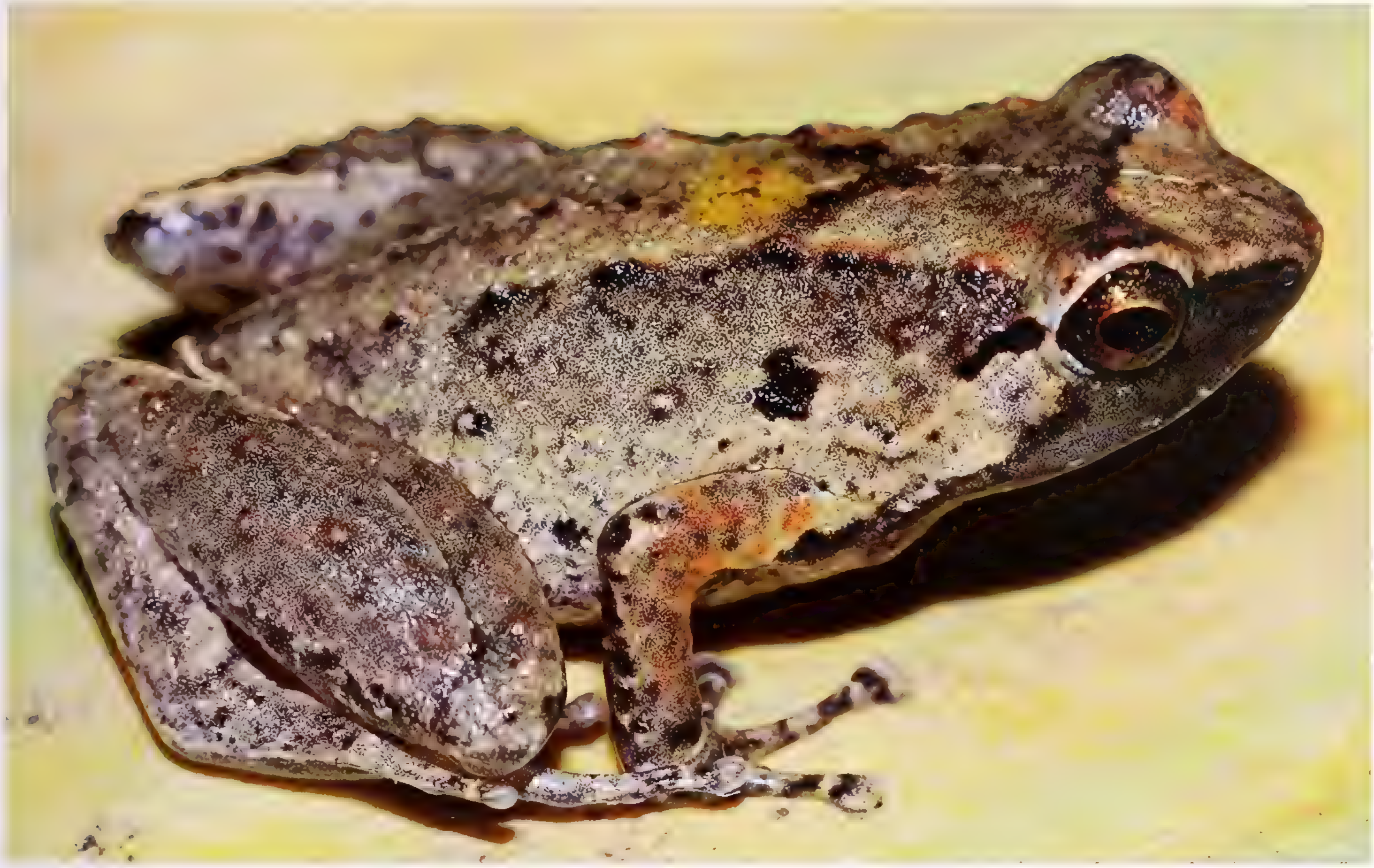

Fig. 5. Dorsolateral view of a more greyish coloured paratype of *Cophixalus monosyllabus* sp. n. (ZMB 74999).

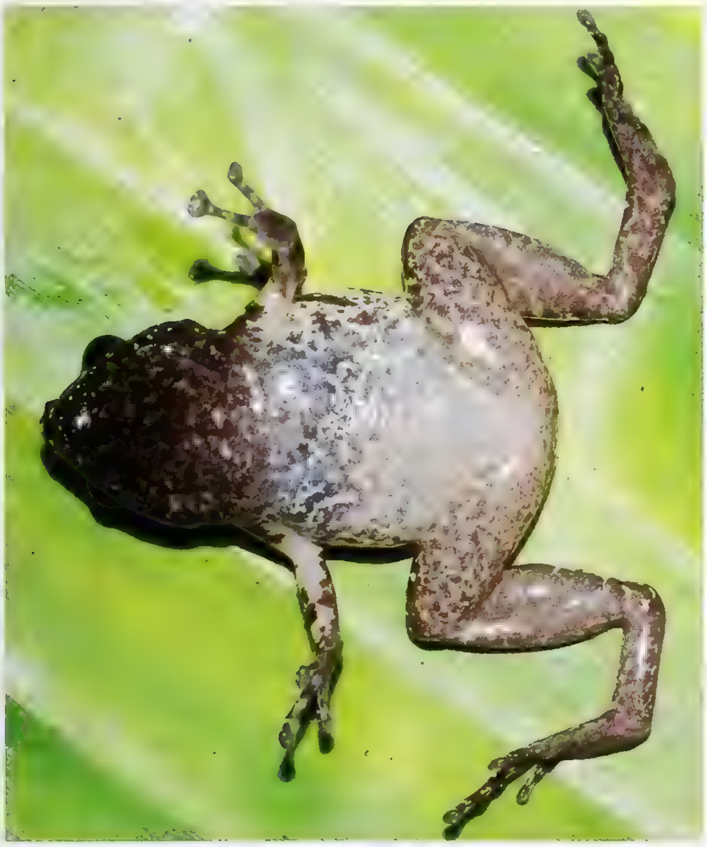

Fig. 6. Ventral view of a paratype of *Cophixalus monosyllabus* sp. n. (ZMB 74995).

slits on both sides of the tongue are entrances to a subgular vocal sac. Legs moderately long, no webs between fingers or toes (Fig. 3); tips of fingers wider than tips of toes, first finger much smaller than other fingers, its tip only scarcely wider than the penultimate phalanx; relative length of fingers 3>2=4>1; third toe clearly longer than the fifth, tip of first toe slightly smaller than tip of the fifth toe, tips of remaining toes clearly wider than that of first and fifth toe; all finger and toe tips with terminal grooves; relative length of toes 4>3>5>2>1, all subarticular tubercles as well as metatarsal and metacarpal tubercles not or only scarcely developed. With exception of some tubercles on flanks, all dorsal, lateral, and ventral surfaces smooth.

Dorsum light brown and clearly demarcated against dark brown upper flanks, dorsal surfaces of legs non-uniform brown, chevron-shaped mark in scapular region, dorsal surface of snout lighter than remaining body; dorsal surfaces of fingers and toes with yellowish, light brown, and dark brown pattern; lateral and dorsolateral flanks with longitudinal rows of blackish spots, a conspicuous blackish spot present also above insertion of foreleg and behind eye; loreal region, tip of snout, and region below and behind eye and underneath tympanum blackish (black face mask); ventral surface of forelegs yellowish with irregu-

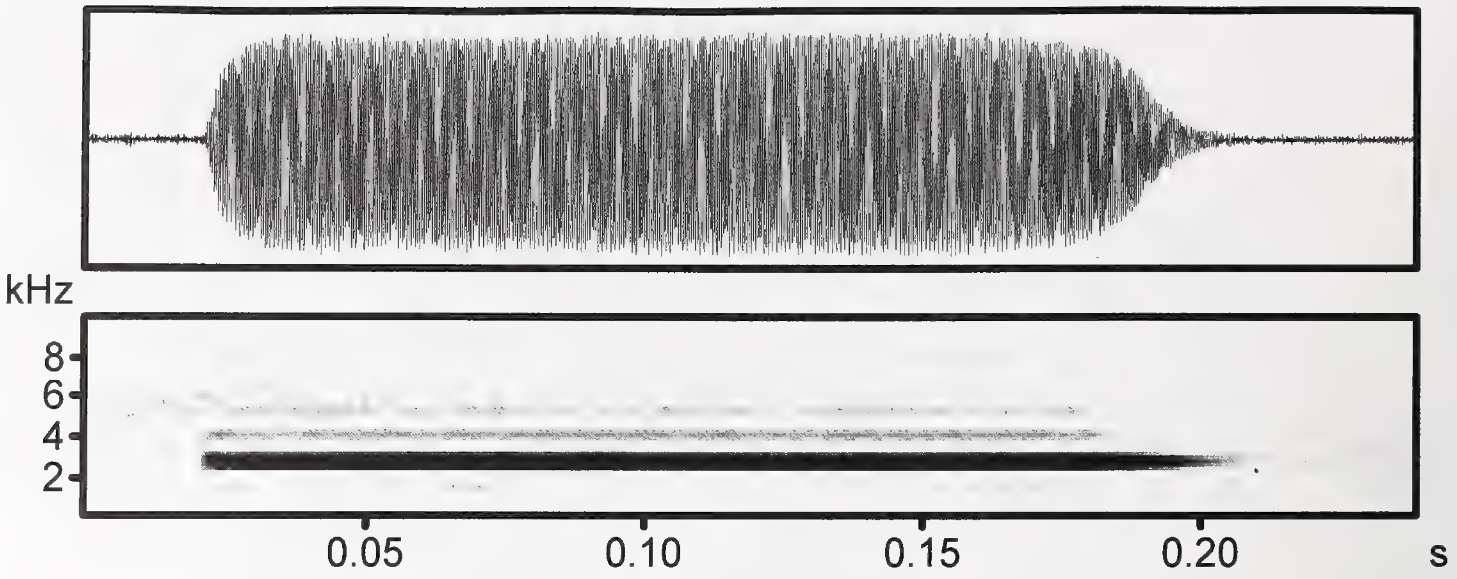

Fig. 7. Wave form (above) and spectrogram (below) of an advertisement call of *Cophixalus monosyllabus* sp. n..

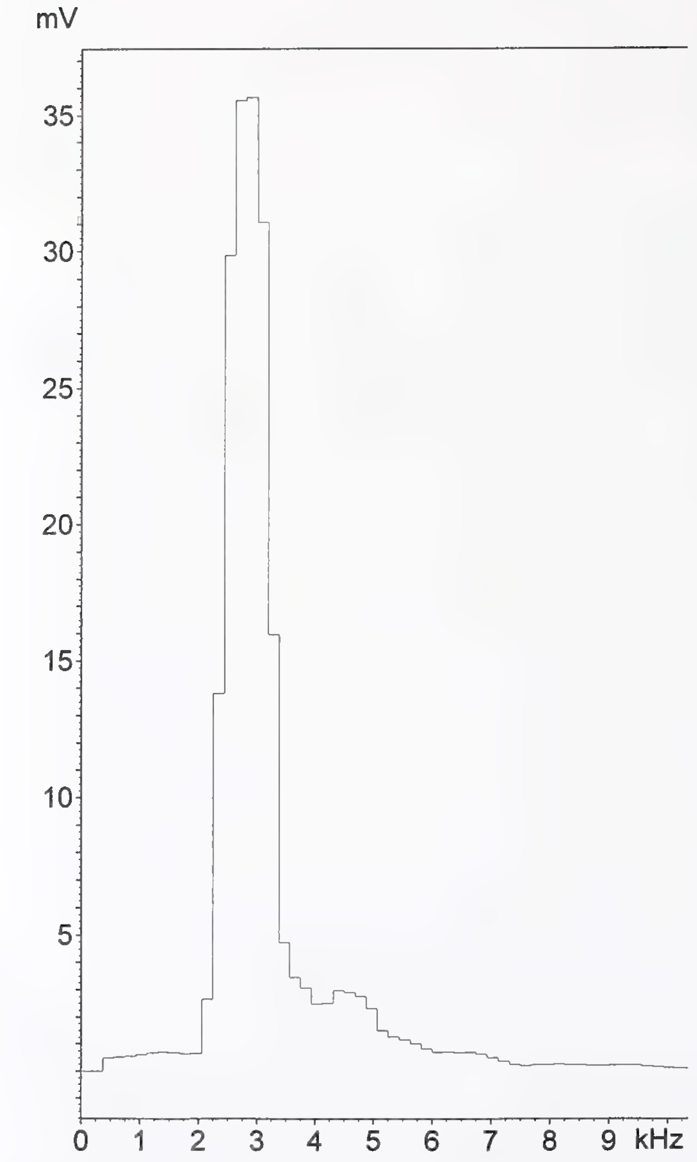

Fig. 8. Power spectrum of an advertisement call of *Cophixalus monosyllabus* sp. n.

lar dark brown flecks, ventral surface of hind legs also yellowish with brown flecks but the latter less intense than on forelegs (ventral skin and muscle tissue of the right thigh was removed for biochemical studies); belly, chest and throat yellowish with brown pigmentation, pigmentation most intense on throat and chest and least intense on abdomen; region around anal opening blackish and region from behind eye, through tympanum, and up to upper arm whitish.

Variation in the type series: Mensural variation for the type series is shown in Table 1. The basic colour and colour pattern elements of all preserved types are fairly uniform and very much resemble those of the holotype. Characteristic elements are a light brown dorsum, which is differentiated from dark brown upper flanks, a dark brown and irregularly pronounced interocular band, a dark chevron or W-shaped mark in the scapular region, a dark face mask, a blackish spot behind eye and above insertion of fore leg, a blackish throat which fades posteriorly into a diffuse dark brown reticulum, and a pale dorsal surface of the snout which is the palest part of all the dorsal surfaces. Only one specimen (ZMB 74996) has a whitish middorsal line from snout tip to anal opening and which continues on to the posterior thighs.

The basic colour in life varies from crème or grey to light brown. Dorsum rather uniform brownish (Fig. 4) or grey (Fig. 5); conspicuous is a blackish or dark brown chevron or W-shaped mark in the scapular region, an irregular dark brown interocular band between posterior parts of eyes, and a crème or light brown coloured dorsal part of snout. Lower flanks are mostly lighter than the remaining lateral areas (Fig. 4). Upper flanks may be of nearly the same

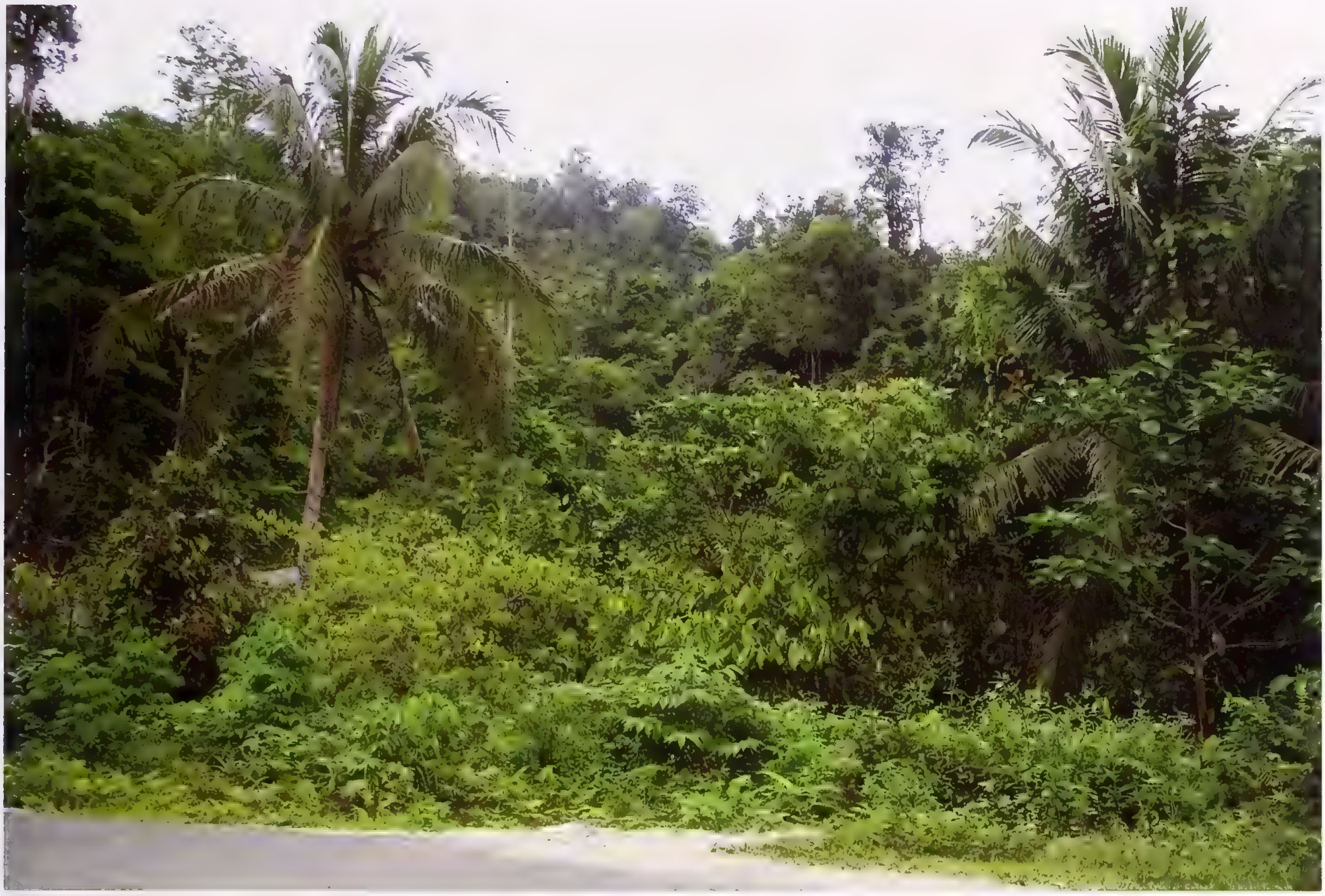

Fig. 9. Habitat of *Cophixalus monosyllabus* sp. n. in the Fakfak Mountains on the Bomberai Peninsula, 700 m a.s.l.

brown or grey colour as on the dorsum. Conspicuous are a blackish spot behind the eye, another blackish spot above the foreleg insertion, and some blackish spots at the border between the dorsum and flanks. It is notable that the dorsum in all preserved specimens is clearly lighter than the upper flanks, whereas the dorsum and upper flanks in most living specimens differed in colour only slightly. Loreal region in all specimens entirely or predominantly black. In some specimens this black area continues to below the eye and extends up to the upper arm, in others this black area ends below the eye. The inner margin of the "upper eyelid" is whitish in most specimens, this colour merging in a broad and light postocular band.

While there are no or only a few tubercles in the preserved specimens, most living specimens exhibited tubercles on the flanks and extremities (rarely on the dorsum). Many of these tubercles have a blackish base and a orange-red cap. Most, and the largest, tubercles are arranged in dorsolateral rows. The yellowish spot posterior of the chevron sign in ZMB 74999 (Fig. 5), which faded to a white spot in preservative, is obviously an exception. Orange-red areas were also found on the forelegs of some specimens. The fine whitish middorsal line in the living specimen in Fig. 5 disappeared completely in fixative. Dorsal sides of legs similarly coloured as other dorsal and dorsolateral body parts. Ventral sides of forearms crème-coloured, its anterior and posterior part covered with irregular dark spots. Throat and chest in all specimens darker than on the remaining ventral surfaces. These dark ventral areas are solidly or discontinuously black or dark brown. Abdomen and ventral sides of hind legs show greater light areas covered by a more or less dense reticulum of grey-brown. Weakest pigmentation was commonly on the posterior abdomen (Fig. 6). Iris yellow-red and nerved by a dense net of blackish lines.

Osteology. One cartilage-bone preparation (ZMB 74997) did not show remarkable differences from that of *Cophixalus tetzlaffi* (see Günther 2003).

Vocalisation. Most calling activities were recorded during rain and damp weather from dusk to 9 p.m. All calls were recorded at temperatures of approximately 21°C. Calls are uttered in series lasting several minutes. The shortest time between two successive calls was about 3 s. Each call consists of a single unpulsed and finely tuned note (Fig. 7). Fifty-six calls (notes) from two males had

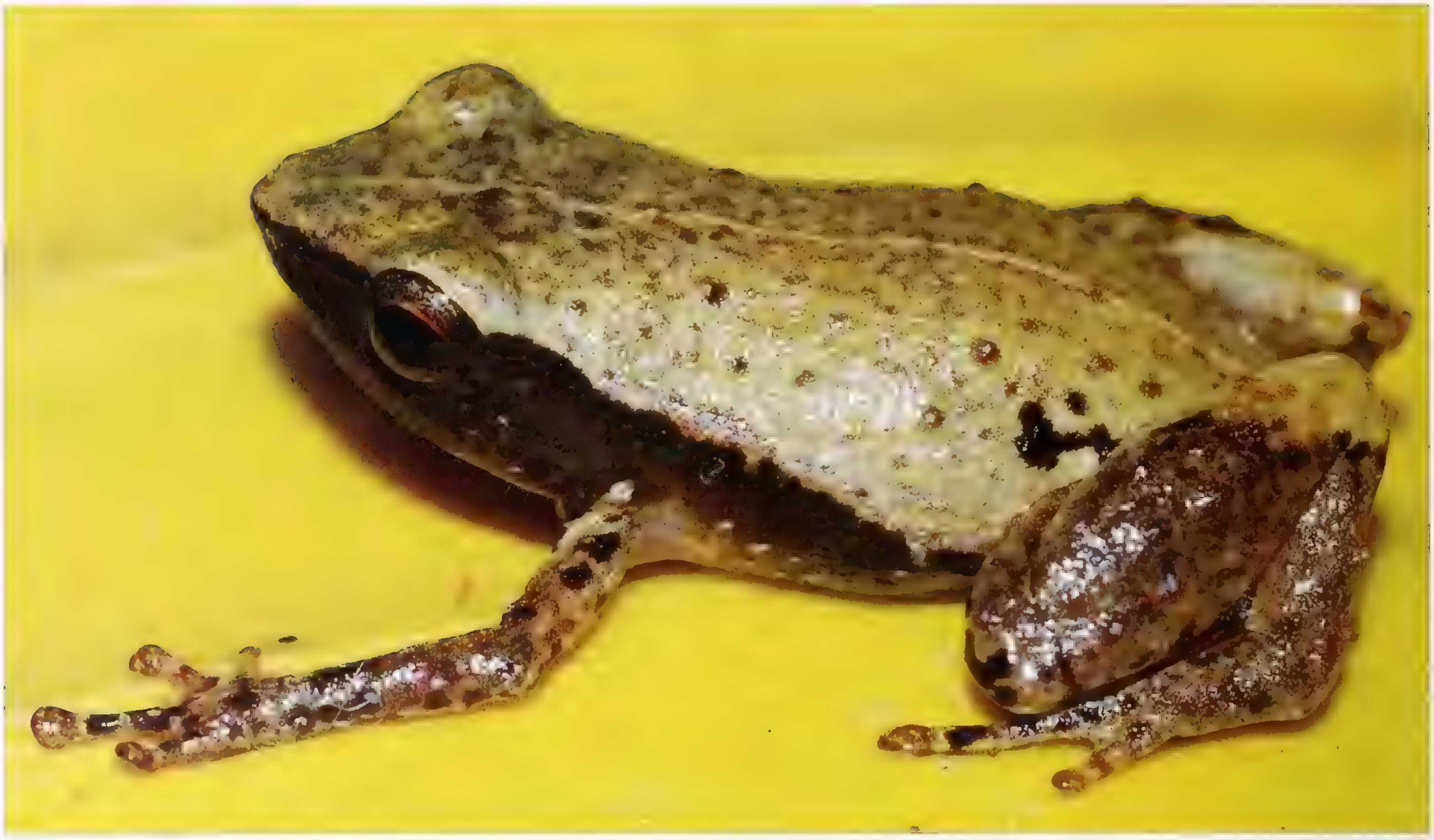

Fig. 10. An undescribed *Cophixalus* species from the Fakfak Mountains, with a 16.9 mm snout-urostyle-length, which at first glance resembles *Cophixalus misimae* recently described by Richards & Oliver (2007) from Misima Island, Louisiade Archipelago, Papua New Guinea.

a mean length of 196 ms, with a minimum of 173 ms and a maximum of 224 ms. Most notes start with a sharp increase in amplitude, and the sound volume may remain constant during the entire note but may also change, with the greatest sound volume mostly near the end. The end of the note occurs more gradually and its exact cessation is fairly difficult to identify (Fig. 7). The dominant frequency is approximately 2.8 kHz (Fig. 8), the fundamental frequency is approximately 1.4 kHz, and the first (and most pronounced) upper harmonic band is at about 4.2 kHz.

Distribution. The new species lives on slopes and in valleys of the southern part of the Fakfak Mountains. We found it along the Fakfak town-Kokas road at elevations of from 250 to 700 m a.s.l. Whether it also occurs in the northern part of the Fakfak Mountains remains to be determined.

Habitat and habits. *Cophixalus monosyllabus* sp. n. lives mostly in the understory (bushes, young trees, and herbs) of taller trees but also in shrubbery without a canopy cover (Fig. 9). The frogs perched mainly on or between living or dead leaves at heights of from one to three meters above the ground. The species is common: we heard several hundred males during a walk of three kilometres along the Fakfak-Kokas road. Some males called at distances of only two m from one another. At favoured places about ten males could be heard calling from one point. For biogeographical reasons it seems worthwhile to mention that at elevations of between 500 and 700 m a.s.l., *C. monosyllabus* sp. n. occurs syntopically with *C. tetzlaffi*, *C. tridactylus,* and another obviously new *Cophixalus* species

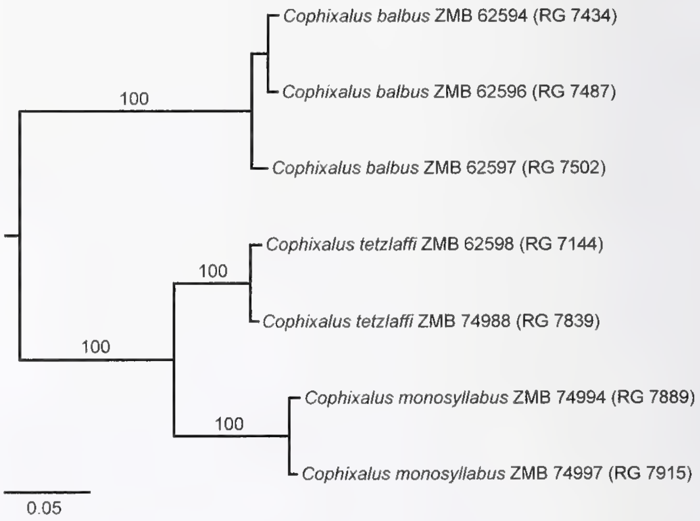
Cophixalus balbus ZMB 62594 (RG 7434)
Cophixalus balbus ZMB 62596 (RG 7487)
Cophixalus balbus ZMB 62597 (RG 7502)
Cophixalus tetzlaffi ZMB 62598 (RG 7144)
Cophixalus tetzlaffi ZMB 74988 (RG 7839)
Cophixalus monosyllabus ZMB 74994 (RG 7889)
Cophixalus monosyllabus ZMB 74997 (RG 7915)
100
100
100
100
0.05

Fig. 11. Bayesian inference phylogram of 16S rRNA. Numbers on branches denote posterior probabilities.

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(Fig. 10). Ecological differences between these four species are the following: *C. monosyllabus* sp. n. occurs at from 250 to 700 m a.s.l. and its calling sites are at between one and three metres above ground; *C. tetzlaffi* occurs at from 400 to 900 m a.s.l. (top of the mountains) and its calling sites are on structures up to one m above the ground; *C. tridactylus* was found at from 500 to 900 m a.s.l. and its calling sites are on the ground; and the obviously new species was found at 860 m a.s.l. in humus soil below the ground surface.

Etymology. The Latin word "monosyllabus" is derived from the Greek composite adjective "monosyllabos" meaning one syllable or monosyllabic, and refers to the advertisement call of the new species which consists of only one uniform note. I dedicate this new species to my dear colleague of many years, Prof. Dr. Wolfgang Böhme, to acknowledge his extraordinary contributions to herpetological science and on the occasion of his retirement from official service, although it is well known that Wolfgang is by no means monosyllabic but rather is very eloquent.

Molecular evidence. According to B. Stelbrink and T. von Rintelen (pers. comm., July 2010) DNA isolation and PCR were done using the protocol of Köhler & Günther (2008). Forward and reverse strands were aligned using CodonCode Aligner v. 3.0.3 (CodonCode Corporation, Dedham, MA, USA) and corrected by eye. Sequences were aligned using MAFFT (Katoh & Toh 2008) and optimized using ALISCORE (Misof & Misof 2009). Phylogenetic analysis (Bayesian inference) was accomplished as conducted by Günther et al (2010).

The analysis of 480 base pairs of the 16S rRNA gene revealed that *Cophixalus monosyllabus* sp. n. is clearly a sister species of *C. tetzlaffi* and both are a sister clade of *C. balbus* (Fig. 11). *C. tridactylus* and *C. humicola* appear more distant in the molecular tree (see also Köhler & Günther 2008), and indicate that the present genus *Cophixalus* most probably is polyphyletic. The genetic distance (uncorrected p-distance) between *C. monosyllabus* sp. n. and *C. tetzlaffi* is 4.3 % for the 16S rRNA gene.

Comparison with other species. *Cophixalus monosyllabus* sp. n. is distinct from other *Cophixalus* species, described up to the year 2003, in the same characters as is *C. tetzlaffi* (Günther 2003). All 16 *Cophixalus* species described after 2003 (Hoskin 2004; Kraus & Allison 2006, 2009; Günther 2006; Richards & Oliver 2007) differ clearly from *C. monosyllabus* sp. n. in body size and also in their advertisement calls. The only species with which *C. monosyllabus* sp. n. can be confused morphologically is *C. tetzlaffi*, especially as both species occur syntopically.

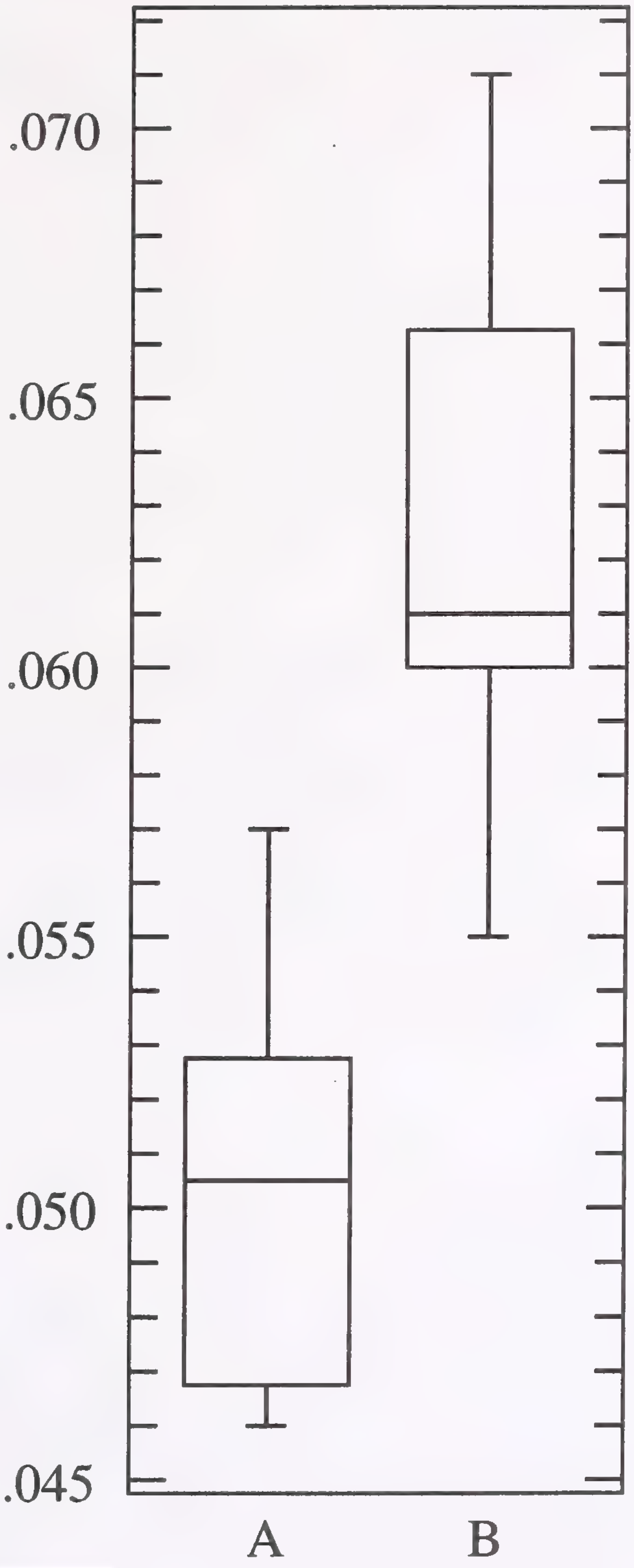

Fig. 12. Box-Whisker-Plot of the ratio "diameter of disc of fourth toe/snout-urostyle-length" (F3D/SUL) in *Cophixalus tetzlaffi* (A) compared to that of *Cophixalus monosyllabus* sp. n. (B).

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I compared the measurements of ten male *C. monosyllabus* sp. n. with that of eight male *C. tetzlaffi* and found the following differences: with a mean body size (SUL) of 23.0 mm (range 20.6–24.3 mm), *C. monosyllabus* sp. n. is somewhat larger than C. *tetzlaffi* (mean 21.4 mm, range 19.5–22.6 mm), Student´s t-test revealed a significant difference with t=2.98 and P=0.0046 in this character; *C. monosyllabus* sp. n. has significantly shorter tibiae than *C. tetzlaffi* (mean of TL/SUL in *C. monosyllabus* sp. n. 0.50, that in *C. tetzlaffi* 0.52, t= 3.39, P=0.0019); *C. monosyllabus* sp. n. has a longer third finger than *C. tetzlaffi* (mean of F3L/SUL in the former 0.27, in the latter 0.26, t=3.01, P=0.0041; *C. monosyllabus* sp. n. has a wider terminal disc on the fourth toe than C. *tetzlaffi* (mean of T4D/SUL in the former 0.054, in the latter 0.046, t=3.11, P=0.0094); *C. monosyllabus* sp. n. has a wider terminal disc on first toe than *C. tetzlaffi* (mean of T1D/SUL in the former 0.027, in the latter 0.018, t=5.63, P=0.00002); *C. monosyllabus* sp. n. has a wider terminal disc on first finger than *C. tetzlaffi* (mean of F1D/SUL in the former 0.021, in the latter 0.015, t=5.36, P=0.00003) and, most significantly, *C. monosyllabus* sp. n. has a wider terminal disc on the third finger than *C. tetzlaffi* (mean of F3D/SUL in the former 0.063, and in the latter 0.051, t=6.14, P=0.000007) (Fig. 12). There are continuous dorsolateral skin ridges in *C. tetzlaffi,* but discontinuous dorsolateral skin glands in *C. monosyllabus* sp. n.

Apart from these morphological differences, and most important for species differentiation, are the advertisement calls: *C. monosyllabus* sp. n. utters a single peeping note with a mean duration of 196 ms (range 173–224 ms), while the call of *C. tetzlaffi* consists of three to four peeping notes with a mean note duration of 422 ms (range 347–518 ms).

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High mitochondrial sequence divergence meets morphological and bioacoustic conservatism: *Boophis quasiboehmei* sp. n., a new cryptic treefrog species from south-eastern Madagascar

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Abstract. We describe a new species of treefrog from Madagascar that is highly similar in external adult morphology, bioacoustics and colouration to *Boophis boehmei* but differs from this species by a remarkable differentiation in a fragment of the mitochondrial 16S rRNA gene. A more detailed analysis revealed that this differentiation is concordant with the pattern in two nuclear genes (Rag1 and POMC) which show no haplotype sharing of the new species with *B. boehmei,* and with a consistent difference in tadpole morphology (third lower row of labial keratodonts reduced in length in the new species). We conclude that concordance between these independent characters indicates two independent evolutionary lineages that should best be considered as separate species, despite their similar adult morphology. The new species, *Boophis quasiboehmei* sp. n., is so far known only from an area in the southern central east and south-east of Madagascar, south of the Mangoro river, while *B. boehmei* is known only from the area around Andasibe north of the river Mangoro. Preliminary data indicate that this group of treefrogs contains several more cryptic species, and a simple explanation assuming the Mangoro river as a barrier being responsible for divergence between them is likely no longer tenable.

Key words. Amphibia, Anura, Mantellidae, *Boophis boehmei, Boophis quasiboehmei* sp. n., Madagascar.

INTRODUCTION

Treefrogs of the genus *Boophis* have long been among Madagascar's less studied amphibians, but intensified fieldwork and application of integrative taxonomy protocols have led to a steep increase of knowledge (Blommers-Schlösser 1979; Cadle 2003; Glaw & Vences 2007; Glaw et al. 2010). Many *Boophis* species call from high positions in the vegetation and intensive nocturnal searches for calling males are needed to find them. Consequently, many species have been described on the basis of only small series or even single individuals, and females are often unknown. Furthermore, many species of *Boophis* are known to be morphologically very similar and a diagnosis based on external morphology alone is often unreliable (Glaw et al. 2001; Vences et al. 2008). However, because the advertisement calls of these species are usually loud and species-specific (Vences et al. 2006), the integration of bioacoustics into their taxonomy has led to an improved understanding of *Boophis* species diversity. Together with an initial screening of molecular diversity, this has led to the description of many new species of *Boophis* (e.g., Andreone 1993, 1996; Andreone et al. 1995; Cadle 1995; Glaw & Thiesmeier 1993; Glaw & Vences 1992, 1994, 1997b, 2002; Glaw et al. 2001, 2010; Köhler et al. 2007, 2008; Vallan et al. 2003, 2010; Vences & Glaw 2002, 2005; Vences et al. 2010; Wollenberg et al. 2008) and the identification of a large number of additional, yet undescribed candidate species (Vieites et al. 2009). Furthermore, tadpoles of *Boophis* are among the most commonly encountered anuran larvae in Malagasy rainforest streams (Vences et al. 2008), and a large number of them have recently been described (e.g., Raharivololoniaina et al. 2006; Randrianiaina et al. 2009a, b).

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Taking the latest species descriptions into account, the genus *Boophis*, classified in the endemic Malagasy-Comoroan family Mantellidae, currently comprises 71 described species. The genus is monophyletic and composed of two main clades that correspond to mainly stream-breeding (subgenus *Boophis*) and pond-breeding species (subgenus *Sahona*), respectively (Glaw & Vences 2006, 2007). The stream breeders are further divided into eight phenetic species groups. Most of these species groups probably are monophyletic units although some are not (particularly the *Boophis majori* group).

The *Boophis goudoti* species group contains 13 small to large species of largely arboreal frogs that are mainly distributed in the rainforests and highlands of Madagascar. A subgroup of small-sized species is characterized by colourful eyes, usually with red iris colour and a bluish iris periphery (Glaw & Vences 1997a, b). Several of these species such as *Boophis boehmei, B. burgeri, B. reticulatus,* and *B. rufioculis* are known to occur at the same locality in the Andasibe region in the northern central east of Madagascar and *B. reticulatus, B.* sp. aff. *rufioculis* and *B.* sp. aff. *boehmei* (= *B.* sp. 8 and *B.* sp. 16 of Vieites et al. 2009) in Ranomafana National Park in the southern central east. Of the various confirmed candidate species in the *B. goudoti* group (Glaw & Vences 2007; Vieites et al. 2009), four have recently been described (or older names were resurrected for them) on the basis of molecular, morphological, and/or bioacoustic differences (Glaw et al. 2010). However, no taxonomic conclusions have so far been drawn for the two candidate species from the Ranomafana region mentioned above (*B.* sp. 8 and *B.* sp. 16), mainly because of their high morphological similarity to *Boophis rufioculis* and to *B. boehmei,* respectively.

Boophis boehmei is the smallest species in the *B. goudoti* group and has been originally described from Andasibe, where it is rather common (Glaw & Vences 1992). Populations from more southern localities, initially allocated to this species (Ranomafana region and Andohahela) turned out to be genetically highly divergent (Vieites et al. 2009) and have therefore been considered as *Boophis* sp. aff. *boehmei* (Glaw & Vences 2007) or *B.* sp. 16 (Vieites et al. 2009), although no reliable morphological or bioacoustic difference between them had been observed. The recent discovery of differences in the tadpole labial tooth row arrangements of *Boophis boehmei* and *Boophis* sp. 16 (Randrianiaina et al. 2009b) prompted us to undertake a more detailed comparison. On the basis of high mitochondrial divergences, consistent differences in two nuclear genes, constant differences in tadpole morphology, and subtle differences in iris colour, we conclude that the central south-eastern populations indeed constitute a distinct species which we describe herein as *Boophis quasiboehmei.* It is however worth to note that *B. boehmei* and the newly described species are indeed among the morphologically and bioacoustically most cryptic species pairs so far discovered in Madagascar.

MATERIALS AND METHODS

Frogs were collected at night by opportunistic searching, using torches and head lamps. Specimens were euthanized in a chlorobutanol solution, fixed in 95% ethanol, and preserved in 70% ethanol. Locality information was recorded with GPS receivers. Specimens were deposited in the collection of Université d'Antananarivo, Département de Biologie Animale, Antananarivo (UADBA), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), and the Zoologische Staatssammlung München (ZSM). FGMV, FGZC and ZCMV refer to F. Glaw and M. Vences field numbers. Terminology for biogeographic regions of Madagascar follows Boumans et al. (2007).

Morphological measurements (in millimetres) were all done by M. Vences with a digital caliper (precision 0.01 mm) to the nearest 0.1 mm. Used abbreviations are: SVL (snout–vent length), HW (greatest head width), HL (head length), ED (horizontal eye diameter), END (eye–nostril distance), NSD (nostril–snout tip distance), NND (nostril–nostril distance), TD (horizontal tympanum diameter), TL (tibia length), HAL (hand length), HIL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus), FORL (forelimb length), and RHL (relative hindlimb length). Terminology and description scheme follow Glaw et al. (2010). Webbing formulae follow Blommers-Schlösser (1979). Statistical analyses were performed with Statistica software (Statsoft Corp., Tulsa, USA).

Vocalizations were recorded in the field using different types of tape recorders (Sony WM-D6C, Tensai RCR-3222) and external microphones (Sennheiser Me-80, Vivanco EM 238), and an Edirol R-09 digital recorder with internal microphones and saved as uncompressed files. Recordings were sampled (or re-sampled) at 22.05 kHz and 16-bit resolution and computer-analysed using the software CoolEdit 98. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points). Spectrograms were obtained at Hanning window function with 256 bands resolution. Temporal measurements are given as range, with mean ± standard deviation in parentheses. Terminology in call descriptions follows Köhler (2000).

Two different molecular data sets were studied:

First, we analyzed sequences of the mitochondrial 16S rRNA gene of around 500 bp from all *Boophis goudoti*

Table 1. Primer sequences and PCR conditions used in the present study. PCR conditions start with temperature (in °C) of each step followed by the time in seconds.

Gene	Primer name	Sequence (5' → 3')	Source	PCR conditions
BDNF	BDNF DRV 1	ACCATCCTTTTCCTKACTATGG	Vieites et al. (2007)	94(120), [94(20), 57(45),
BDNF	BDNF DRV 1	CTATCTTCCCCTTTTAATGGTC	Vieites et al. (2007)	72(120) 39], 72(600)
Rag1	Amp F2	ACNGGNMGICARATCTTYCARCC	s. Chiari et al. (2004)	94(120), [94(20), 50(50),
Rag1	Amp R2	GGTGYTTYAACACATCTTCCATYTCRTA	s. Chiari et al. (2004)	72(180) x 45], 72 (600)
POMC	POMC DRV F1	ATATGTCATGASCCAYTTYCGCTGGAA	Vieites et al. (2007)	95(120), [95(60), 58(60),
POMC	POMC DRV R1	GGCRTTYTTGAAWAGAGTCATTAGWGG	Vieites et al. (2007)	72(90) x 35], 72(600)

group species and candidate species with reddish iris colour as obtained by Vieites et al. (2009), Randrianiaina et al. (2009b) and Strauß et al. (2010). After alignment and removal of incomplete sections at its beginning and end the data set for analysis had a length of 479 bp. Unpartitioned Bayesian inference searches were performed. The best model of evolution (GTR+G) was determined by AIC in MrModeltest (Nylander 2002). Bayesian analyses were performed with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Two runs of 10 million generations (started on random trees) and four incrementally heated Markov chains (using default heating values) each, sampling the Markov chains at intervals of 1000 generations were used. The last 5001 trees were retained post burn-in and summarized to generate the majority rule consensus tree.

Second, we used tissue samples of four and one *Boophis boehmei* from Andasibe and An'Ala, respectively, and four and two tissue samples of *B. quasiboehmei* from Sahamalaotra (=Samalaotra) and Ambohitsara (Tsitolaka forest) for newly determining DNA sequences of various nuclear genes. Toe clips or leg muscle tissue samples (preserved in 95% ethanol) were used for DNA extraction. Total genomic DNA was extracted from the tissue samples using proteinase K digestion (10 mg/ml concentration) followed by a standard salt extraction protocol (Bruford et al. 1992). We amplified fragments of three genes from the nuclear DNA (nuDNA): brain-derived neurotrophic factor (BDNF), recombination activating gene 1 (Rag1), and pro-opiomelanocortin (POMC). Standard Polymerase chain reactions were performed in a final volume of 11 µl and using 0.3 µl each of 10 pmol primer, 0.25 µl of total dNTP 10 mM (Promega), 0.08 µl of 5 U/ml GoTaq, and 2.5 µl 5X Green GoTaq Reaction Buffer (Promega). Primers and detailed PCR conditions are provided in Table 1. PCR products were then purified through QIAquick purification kit (Qiagen) according to the manufacturer's instruction. Purified PCR templates were sequenced on an automated DNA sequencer (Applied Biosystems ABI 3130XL). Chromatographs were checked and sequences were edited using CodonCode Aligner (v. 2.0.6, Codon Code Corporation). All newly determined sequences have been deposited in GenBank (HQ380132-HQ380172). Haplotypes of POMC data were inferred using the PHASE algorithm (Stephens et al. 2001) implemented in DnaSP software (Version 5.10.3; Librado & Rozas 2009). Haplotype network reconstruction of phased sequences of the POMC (Fig. 2A) and Rag1 (Fig. 2B) fragments were performed using the software TCS, version 1.21 (Clement et al. 2000). This software employs the method of Templeton et al. (1992) and it calculates the number of mutational steps by which pairwise haplotypes differ, computing the probability of parsimony for pairwise differences until the probability exceeds 0.95 (no manual adjustment of threshold was necessary).

RESULTS

A detailed analysis of all available 16S rRNA sequences of adults and tadpoles assigned to *B. boehmei* (GenBank accession numbers GQ904739–GQ904746, DQ792470–DQ792471, AY341717, AY848560–AY848562) and the candidate species *B.* sp. 16 (sensu Vieites et al. 2009) (accession numbers GQ904717–GQ904738, AY848529–AY848536) confirmed that these two forms are genetically highly divergent. Depending on the length of the sequence available, the uncorrected pairwise distances were between 8.8% and 11.0% (note that these values are higher than the 6.8% reported by Vieites et al. (2009) because of different lengths of the sequences, with a different proportion of hypervariable sites included in the analysis). Next to single substitutions we also detected one major insertion of seven nucleotides in the candidate species which in this extent was not present in any of the related species of *Boophis* (Fig. 1). Pairwise divergences were 0.0–0.9% within *B. boehmei,* 0.0–0.5% within specimens of *B.* sp. 16 from the Ranomafana region, and 3.6–4.9% between the single available sequence of *B.* sp. 16 from Andohahela

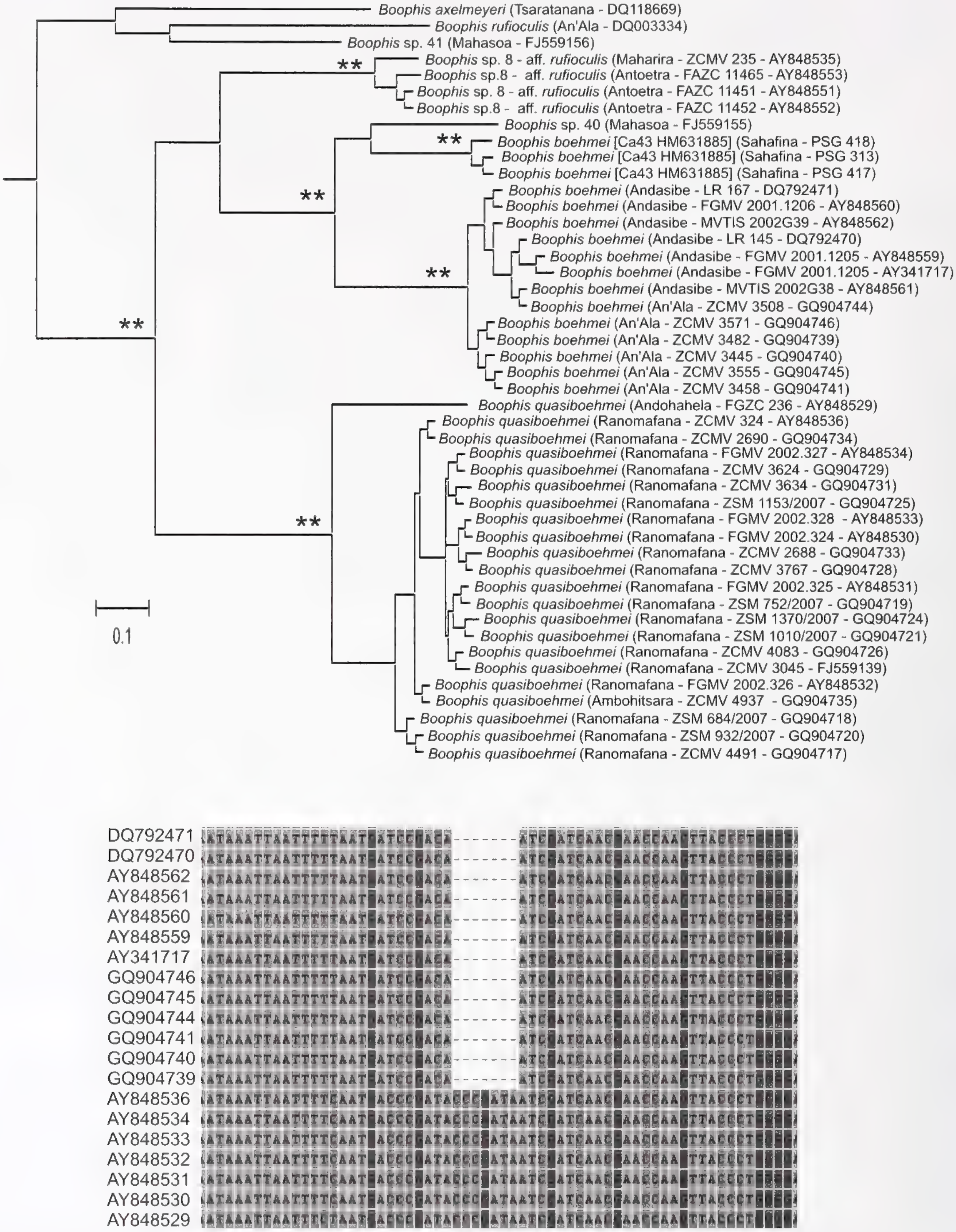
Boophis axelmeyeri (Tsaratanana - DQ118669)
Boophis rufioculis (An'Ala - DQ003334)
Boophis sp. 41 (Mahasoa - FJ559156)
**
Boophis sp. 8 - aff. rufioculis (Maharira - ZCMV 235 - AY848535)
Boophis sp.8 - aff. rufioculis (Antoetra - FAZC 11465 - AY848553)
Boophis sp. 8 - aff. rufioculis (Antoetra - FAZC 11451 - AY848551)
Boophis sp.8 - aff. rufioculis (Antoetra - FAZC 11452 - AY848552)
Boophis sp. 40 (Mahasoa - FJ559155)
**
Boophis boehmei [Ca43 HM631885] (Sahafina - PSG 418)
Boophis boehmei [Ca43 HM631885] (Sahafina - PSG 313)
Boophis boehmei [Ca43 HM631885] (Sahafina - PSG 417)
**
Boophis boehmei (Andasibe - LR 167 - DQ792471)
Boophis boehmei (Andasibe - FGMV 2001.1206 - AY848560)
Boophis boehmei (Andasibe - MVTIS 2002G39 - AY848562)
Boophis boehmei (Andasibe - LR 145 - DQ792470)
Boophis boehmei (Andasibe - FGMV 2001.1205 - AY848559)
Boophis boehmei (Andasibe - FGMV 2001.1205 - AY341717)
**
Boophis boehmei (Andasibe - MVTIS 2002G38 - AY848561)
Boophis boehmei (An'Ala - ZCMV 3508 - GQ904744)
Boophis boehmei (An'Ala - ZCMV 3571 - GQ904746)
**
Boophis boehmei (An'Ala - ZCMV 3482 - GQ904739)
Boophis boehmei (An'Ala - ZCMV 3445 - GQ904740)
Boophis boehmei (An'Ala - ZCMV 3555 - GQ904745)
Boophis boehmei (An'Ala - ZCMV 3458 - GQ904741)
Boophis quasiboehmei (Andohahela - FGZC 236 - AY848529)
Boophis quasiboehmei (Ranomafana - ZCMV 324 - AY848536)
Boophis quasiboehmei (Ranomafana - ZCMV 2690 - GQ904734)
Boophis quasiboehmei (Ranomafana - FGMV 2002.327 - AY848534)
Boophis quasiboehmei (Ranomafana - ZCMV 3624 - GQ904729)
Boophis quasiboehmei (Ranomafana - ZCMV 3634 - GQ904731)
Boophis quasiboehmei (Ranomafana - ZSM 1153/2007 - GQ904725)
Boophis quasiboehmei (Ranomafana - FGMV 2002.328 - AY848533)
**
Boophis quasiboehmei (Ranomafana - FGMV 2002.324 - AY848530)
Boophis quasiboehmei (Ranomafana - ZCMV 2688 - GQ904733)
Boophis quasiboehmei (Ranomafana - ZCMV 3767 - GQ904728)
Boophis quasiboehmei (Ranomafana - FGMV 2002.325 - AY848531)
Boophis quasiboehmei (Ranomafana - ZSM 752/2007 - GQ904719)
Boophis quasiboehmei (Ranomafana - ZSM 1370/2007 - GQ904724)
0.1
Boophis quasiboehmei (Ranomafana - ZSM 1010/2007 - GQ904721)
Boophis quasiboehmei (Ranomafana - ZCMV 4083 - GQ904726)
Boophis quasiboehmei (Ranomafana - ZCMV 3045 - FJ559139)
Boophis quasiboehmei (Ranomafana - FGMV 2002.326 - AY848532)
Boophis quasiboehmei (Ambohitsara - ZCMV 4937 - GQ904735)
Boophis quasiboehmei (Ranomafana - ZSM 684/2007 - GQ904718)
Boophis quasiboehmei (Ranomafana - ZSM 932/2007 - GQ904720)
Boophis quasiboehmei (Ranomafana - ZCMV 4491 - GQ904717)
DQ792471
DQ792470
AY848562
AY848561
AY848560
AY848559
AY341717
GQ904746
GQ904745
GQ904744
GQ904741
GQ904740
GQ904739
AY848536
AY848534
AY848533
AY848532
AY848531
AY848530
AY848529

Fig. 1. Phylogenetic tree of species and candidate species of the *Boophis goudoti* group with red iris colour, obtained using Bayesian inference based on DNA sequences of the mitochondrial 16S rRNA gene (alignment length 479 bp). Bayesian posterior values >0.95 symbolized by a single asterisk, of 0.99-1.00 by two asterisks. For each sequence, locality, voucher number and Genbank number are given in parentheses. *Boophis goudoti* was used as outgroup (not shown). Note that the deeper phylogenetic relationships shown are not reliable due to the limited amount of sequence information used in the analysis, and according to an unpublished multi-gene data set of K. C. Wollenberg, *B. boehmei* and *B. quasiboehmei* are probably sister groups. The alignment in the lower part of the figure shows a section of the 16S alignment, with sequences of *Boophis boehmei* (upper 13 sequences; numbers to the left are Genbank accession numbers) and *Boophis quasiboehmei* (lower seven sequences). The insertion of seven nucleotides is a synapomorphy of all *B. quasiboehmei* specimens for which a sequence was obtained, and in this extent is lacking also in all other species of the *B. goudoti* group.

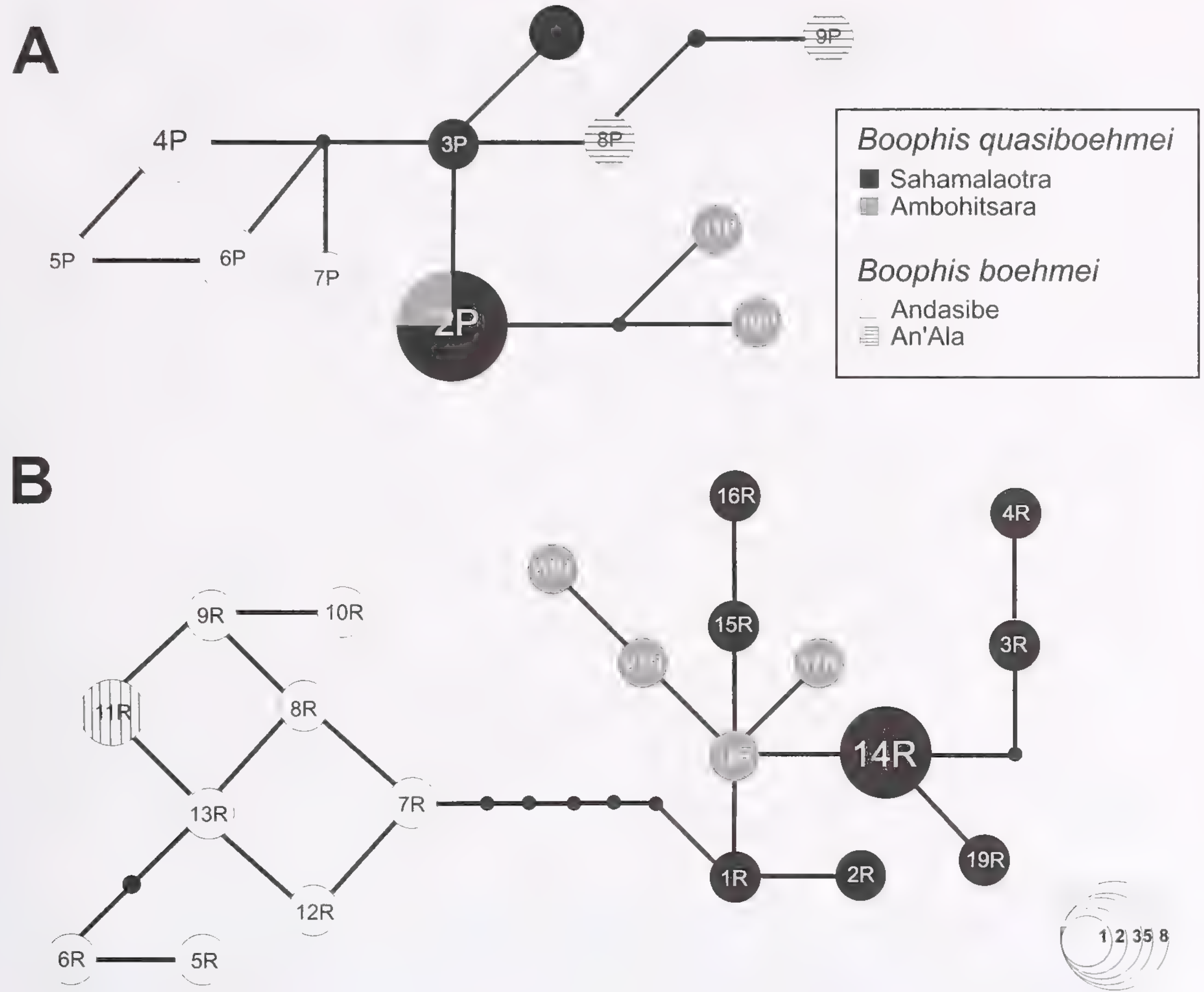

Fig. 2. Haplotype networks of the nuclear POMC (A) and Rag1 (B) genes fragments in *B. boehmei* and *B. quasiboehmei*, each from two different localities. Haplotypes per each individual were inferred using the Phase algorithm. The networks show complete absence of haplotype sharing among the two taxa.

(AY848529) and those from Ranomafana. Genetically identified specimens assigned to *B. boehmei* were from Andasibe and An'Ala. Specimens from Sahafina (Gehring et al. 2010) had quite divergent DNA sequences and their status is unclarified, but they clustered with *B. boehmei* (Fig. 1). Following the scheme suggested by Padial et al. (2010), this population was considered a new unconfirmed candidate species *Boophis boehmei* [Ca43 HM631885] by Gehring et al. (2010). Probably, specimens from Ankeniheny for which no molecular data are available belong to this species as well. Specimens assigned to *B.* sp. 16 were from the Ranomafana area (including Ambatovory, Sahamalaotra, Imaloka, Kidonavo, Vohiparara) and Ambohitsara, as well as from Andohahela.

Besides a simple assessment of molecular divergences between *Boophis* sp. 16 and *B. boehmei* it is also necessary to comment on its phylogenetic position. The analysis of Vieites et al. (2009) placed *B. boehmei* with *B.* sp. 8 from Ranomafana and *B.* sp. 40 from Mahasoa forest, and the clade made up by these species was sister to *B.* sp. 16. Our analysis (Fig. 1) included sequences of all these taxa and confirmed the phylogenetic relationships suggested by Vieites et al. (2009). However, an unpublished analysis based on multiple mitochondrial genes by K.C. Wollenberg instead suggested a probable sister-group relationship between *B. boehmei* and *B.* sp. 16, confirming that the 16S rRNA gene alone as used here is insufficient to clarify the phylogeny among *Boophis* species. Altogether, the phylogenetic relationships among all these species require a much more detailed analysis which however is beyond the scope of the present paper.

The results of the mitochondrial marker indicate no or limited gene flow between *B. boehmei* and *B.* sp. 16. This result was corroborated by the analysis of two nuclear markers (Fig. 2; the conserved BDNF gene showed no variation). While in POMC (Fig. 2A), the single included An'Ala specimen had a different haplotype not clustering with those of Andasibe, in Rag1 the haplotypes belonging to the two species formed two well-defined clusters separated from each other by a minimum of six mutation-

Table 2. Morphometric measurements (all in mm) of examined voucher specimens of *Boophis boehmei* and *B. quasiboehmei*. For abbreviations of morphometric measurements and collection acronyms see Materials and Methods. Additional abbreviations: HT, holotype; PT, paratype; M, male; F, female. RHL (relative hindlimb length) is coded as follows: when hindlimb is adpressed along body, tibiotarsal articulation reaches (1) anterior eye corner, (2) nostril, (3) between nostril and snout tip, (4) snout tip, (5) beyond snout tip.

Number	Field number	Type	Locality	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	RHL
B. boehmei	–																		
ZFMK 53642	–	HT	Andasibe	M	29.4	11.3	11.9	2.0	3.9	2.4	2.3	3.2	17.9	9.0	48.4	21.2	12.4	16.4	2
ZSM 563/1999	(ZFMK 53643)	PT	Andasibe	M	28.4	10.9	11.4	2.2	3.9	2.3	2.4	3.4	17.2	8.5	46.5	20.9	11.8	15.2	2
ZFMK 52637	–	PT	Andasibe	M	27.8	10.8	11.5	2.0	4.0	2.2	2.3	3.0	17.1	8.5	46.6	19.9	11.2	15.3	2
ZFMK 52638	–	PT	Andasibe	M	28.7	11.4	11.7	2.1	4.2	2.3	2.4	3.6	18.2	8.9	49.2	20.6	12.3	14.9	2
ZFMK 52639	–	PT	Andasibe	M	28.5	10.7	11.6	2.0	3.6	2.2	2.2	3.0	18.4	9.3	49.3	21.3	12.5	15.6	2
ZSM 304/2000	–	–	Andasibe	M	29.0	11.5	11.9	2.1	4.4	2.5	2.4	3.4	19.0	9.2	50.2	22.1	12.7	16.1	4
ZSM 22/2002	FGMV 2001.1191	–	Andasibe	M	30.8	10.7	11.4	2.0	4.0	2.3	2.4	3.0	18.4	9.6	48.5	21.6	12.8	15.2	2
ZSM 23/2002	FGMV 2001.1193	–	Andasibe	M	30.6	11.5	12.0	2.2	4.0	2.5	2.5	3.6	19.3	9.4	50.3	21.6	12.5	15.6	2
ZSM 24/2002	FGMV 2001.1195	–	Andasibe	M	28.5	11.0	11.4	2.0	4.2	2.4	2.3	3.3	19.0	8.7	47.6	20.3	12.0	14.9	2
ZFMK 50649	–	–	Andasibe	M	28.8	10.6	10.9	2.2	4.1	2.3	2.6	3.4	16.4	8.6	48.8	20.8	12.3	15.4	4
ZFMK 50650	–	–	Andasibe	M	30.3	11.1	11.4	2.1	4.4	2.4	2.7	3.9	19.2	9.3	50.3	22.4	12.7	16.3	2
ZFMK 60084	–	–	An'Ala	M	27.6	10.6	11.1	2.0	4.2	2.2	2.7	3.3	17.3	8.2	47.8	20.6	12.1	15.2	5
ZSM 25/2002	FGMV 2001.1206	–	Andasibe	F	37.7	14.0	15.2	2.3	5.0	3.1	3.0	4.6	24.9	11.9	62.5	27.9	15.9	20.2	5
ZSM 225/2006	ZCMV 2400	–	An'Ala	F	41.5	14.7	14.9	3.3	5.0	3.3	3.3	4.4	25.1	12.3	63.7	28.7	16.8	20.0	1
ZFMK 60028	–	–	Andasibe	F	40.6	14.8	15.4	2.9	4.3	3.7	3.5	4.2	24.0	11.8	65.5	28.8	17.3	21.1	2
ZFMK 60029	–	–	Andasibe	F	41.6	14.6	14.9	2.4	5.0	3.2	3.4	3.9	24.2	12.0	62.8	28.8	17.3	19.8	1
B. quasiboehmei																			
ZSM 227/2006	ZCMV 3045	HT	Ambatovory	M	26.7	10.6	11.2	2.0	3.7	2.3	2.3	3.3	17.7	9.1	48.1	20.8	11.1	15.2	5
ZSM 715/2003	FG/MV 2002-0363	PT	Vohiparara	M	28.8	10.6	11.0	1.9	3.7	2.3	2.5	3.7	18.4	9.0	48.0	20.8	11.9	15.5	2
ZSM 224/2006	ZCMV 2988	PT	Sahamalaotra	M	27.5	10.7	11.6	1.9	4.1	2.5	2.5	3.3	17.8	8.8	48.2	21.1	12.0	15.1	4
ZSM 226/2006	ZCMV 2951	PT	Imaloka	M	28.6	10.7	11.3	1.8	3.9	2.2	2.0	3.3	18.8	9.6	50.9	22.8	12.7	16.2	5
ZSM 228/2006	ZCMV 3051	PT	Ambatovory	M	29.3	11.2	11.6	1.8	4.1	2.4	2.6	3.4	20.5	9.9	50.9	22.9	13.2	16.2	2
ZSM 229/2006	ZCMV 3069	PT	Ambatovory	M	28.6	11.1	11.1	2.0	3.9	2.3	2.4	3.2	19.0	9.6	51.3	22.6	12.5	15.8	5
ZSM 230/2006	ZCMV 3070	PT	Ambatovory	M	28.4	10.7	11.5	2.1	3.9	2.6	2.7	3.2	17.9	9.4	49.3	21.8	12.8	15.4	2
ZSM 231/2006	ZCMV 3360	PT	Ranomena	M	27.8	10.5	11.0	2.0	3.9	2.3	2.7	3.3	17.5	8.4	45.9	20.4	12.0	14.3	2
ZSM 232/2006	ZCMV 3374	PT	Ranoma-fanakely river (?)	M	28.9	10.7	11.2	1.9	4.0	2.3	2.7	3.2	18.3	9.1	48.5	21.3	12.6	15.5	3
ZFMK 59881	–	PT	Ranomafana region	M	29.2	11.5	11.8	2.0	4.1	2.6	2.8	3.6	18.0	9.6	49.5	22.5	13.3	16.6	3
ZFMK 59882	–	PT	Ranomafana region	M	29.3	11.1	11.3	1.9	4.0	2.3	2.4	3.7	18.2	9.4	48.3	21.6	13.1	15.4	2
ZSM 178/2006	BOR 1079?	–	Befotaka-Midongy	M	30.8	11.5	11.9	1.9	4.2	2.3	3.0	3.8	19.1	9.8	50.4	22.1	12.8	16.0	3

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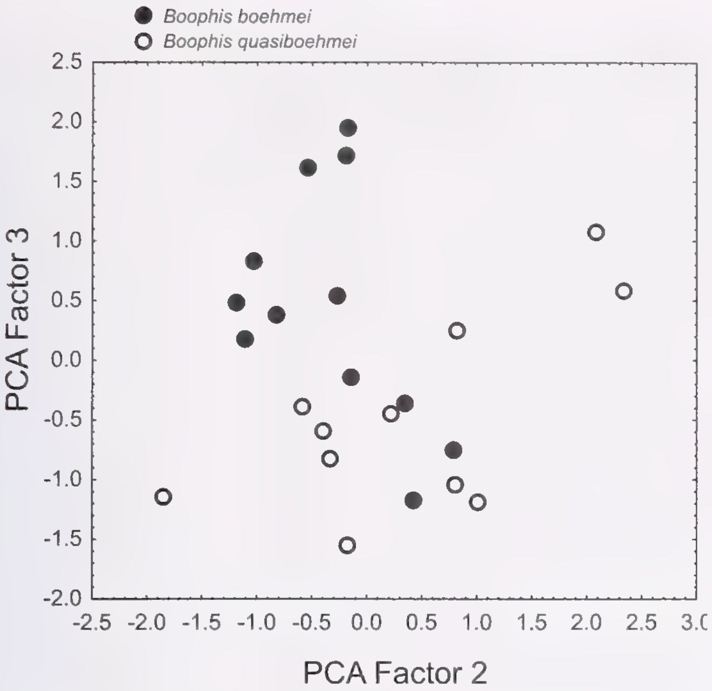

Fig. 3. Scatterplot of individual males of *Boophis boehmei* (filled circles) and *B. quasiboehmei* (open circles) along the second and third factor of a Principal Component Analysis (Varimax normalized rotation). The PCA was based on measurements in Table 1. The specimen from Midongy was excluded from analysis because the species identity of this population is not fully clarified.

al steps. Although the nuclear data set refers to only a limited number of specimens, the fact that there is no haplotype sharing between the two forms suggests that they represent independent evolutionary lineages.

Nevertheless, these pronounced genetic divergences were contrasted by no or low divergences in adult morphology and bioacoustics. The calls of the two forms were similar, with no detectable differences (see call descriptions below). In both forms, notes may be combined to short regular series, and intervals between notes are otherwise highly variable and mostly irregular. The temporal and spectral parameters in calls of both forms are somewhat variable among populations and individuals, but broadly overlap at inter- and intra-populational level. Even the pulse rate within notes, a character shown to be evolutionary highly dynamic among closely related species (e.g. Padial et al. 2008), is identical in both forms (see analysis below). Inter-note intervals outside of regular note series furthermore seem to depend on calling motivation of the individual male.

A close examination of adult morphology yielded no discrete characters that would allow a diagnosis between the two forms. One subtle difference was detected in adult life

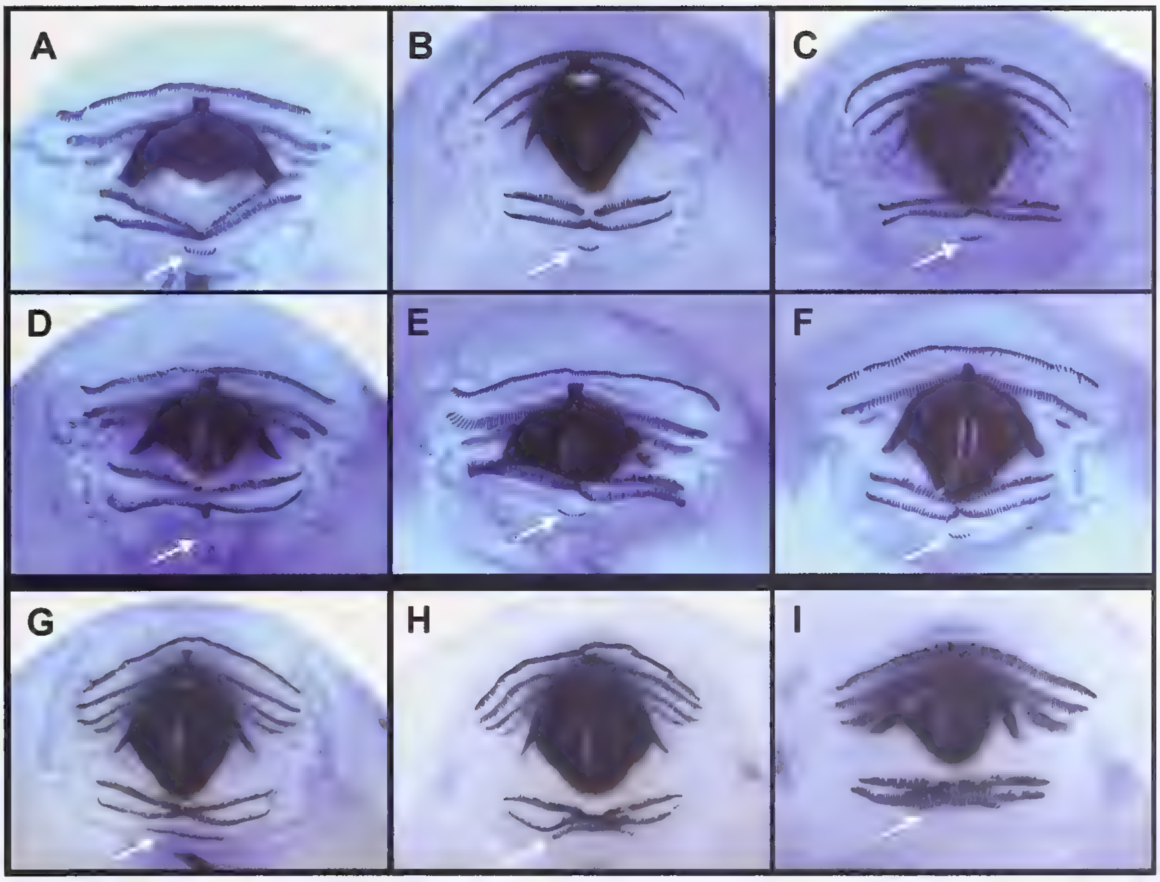

Fig. 4. Comparative photographs of oral discs of preserved tadpoles of *Boophis quasiboehmei* sp. n. (top, A–F) and *Boophis boehmei* (bottom, G–I): (A) ZSM 442/2008, Imaloka; (B–C) ZSM 83–84/2008, Ambohitsara; (D) ZSM 509/2008, Ambatolahy; (E) ZSM 1682/2007, Sahalamaotra; (F) ZSM 443/2008, Imaloka; (G–I) ZSM 1738/2007, 1750/2007, 1779/2007, An'Ala. Note the short third lower (= posterior) keratodont row of *Boophis quasiboehmei* sp. n. with only few (or even misssing [D]) keratodonts, and the less reduced legth of this row in *B. boehmei* (indicated by white arrows). In the tadpoles of other species of the *Boophis goudoti* group, the third lower keratodont row is more extended than in the two species shown (see Randrianiaina et al. 2009b).

Table 3. Factor loadings, Eigenvalues and percent explained variation from a Principal Component Analysis of morphometric data in Table 2. Factor loadings >0.5 are shown in bold.

	Factor 1	Factor 2	Factor 3	Factor 4
SVL	**0.535637**	0.024396	0.278024	0.432915
HW	0.401178	-0.052815	**0.722325**	0.434988
HL	0.283729	-0.059521	**0.901536**	-0.000783
TD	-0.451112	0.171742	**0.508941**	0.315946
ED	0.042109	0.184460	0.248786	**0.727413**
END	0.263940	**0.645782**	**0.593063**	0.078554
NSD	-0.058373	**0.886713**	-0.111786	0.323847
NND	0.169004	0.159007	-0.021443	**0.796064**
FORL	**0.776970**	-0.189957	0.113991	0.209375
HAL	**0.936216**	0.015471	0.113066	-0.107870
HIL	**0.852890**	-0.051712	0.150553	0.154111
FOTL	**0.932469**	0.147455	0.044485	0.068645
FOL	**0.784388**	0.333820	0.095038	0.209488
TIBL	**0.743402**	0.023610	0.266693	0.084073
Eigenvalue	5.977193	2.369640	1.412833	0.905600
% Variance	42.69424	16.92600	10.09166	6.46857

colouration. All specimens of *B. boehmei* had a bright red outer iris area and a brownish inner iris area, whereas *B.* sp. 16 had no such bright red colour but orange, either as a more or less uniformly orange iris or as an orange outer iris area.

In a search for a possible morphometric differentiation, we carried out a Principal Component Analysis on the basis of measurements in Table 2 (males only). The analysis resulted in three factors with Eigenvalues greater than 1 (Table 3) which together explained 70% of the total variation. Because size of specimens was similar, the first factor was not representative mainly of body size, but of relative limb length; the highest factor loadings were for variables associated with limb length (Table 3). Factors 2 and 3 were associated with the shape of the head: Factor 2 with END and NSD, and Factor 3 with mainly HW and HL. While Factor 1 resulted only marginally in a trend of separation of the two species (not shown), Factors 2 and especially 3 separated most specimens of *B. boehmei* vs. *B.* sp. 16 (Fig. 3). However, univariate analyses on the basis of the variables with highest factor loadings did not result in a convincing separation (not shown), indicating that morphometric data cannot serve as diagnostic characters to separate these two forms.

The most convincing diagnostic character comes from tadpole morphology and has been described in detail by Randrianiaina et al. (2009a, b): all tadpoles of *Boophis* sp. 16 (from Ranomafana and Ambohitsara; N = 75) examined had a short (or completely absent) third posterior row of labial keratodonts (P3), whereas in *B. boehmei* (from localities Andasibe and An'Ala) this row was slightly shorter than in other species of the *B. goudoti* group, but still much longer than in *B.* sp. 16, with no overlap in numbers of labial keratodonts in P3 and almost no overlap in relative length of P3 (Fig. 4).

Given this constant difference in tadpole morphology which fully correlates with high mitochondrial divergences (among the highest observed between closely related mantellid frog species), and with fully separated haplotypes in two nuclear genes, we conclude that *B. boehmei* and *B.* sp. 16 constitute two separate and independent evolutionary lineages. Therefore, they should best be considered as distinct species, although cryptic in adult morphology and advertisement calls. In the following we thus describe *B.* sp. 16 as a new species.

***Boophis quasiboehmei* sp. n.**
(Figs 5–6)

Holotype. ZSM 227/2006 (field number ZCMV 3045), adult male (Fig. 5), collected at Ambatovory, at the edge of Ranomafana National Park, south-eastern Madagascar, 21°14,279' S, 47°25,487' E, 966 m a.s.l., on 26 February 2006 by M. Vences, Y. Chiari, T. Rajoafiarison, E. Rajeriarison, P. Bora and T. Razafindrabe.

Paratypes. ZFMK 59881–59882, two adult males, collected in the Ranomafana region, south-eastern Madagascar, in December 1994 by M. Burger; ZSM 715/2003 (FG/MV 2002-0363), one adult male, collected at Vohiparara (close to the Kidonavo bridge), Ranomafana National Park, 21°13' S, 47°22' E, ca. 1000 m a.s.l., on 20 January 2003, by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas and D. R. Vieites; ZSM 228/2006 (ZCMV 3051), ZSM 229/2006 (ZCMV 3069), and ZSM 230/2006 (ZCMV 3070), three adult males, from same locality and with same collectors and collection date; ZSM 224/2006 (ZCMV 2988), male, collected at Sahamalaotra, Ranomafana National Park, south-eastern Madagascar, 21°14.113' S, 47°23.767' E, south-eastern Madagascar, on 25 February 2006 by M. Vences, Y. Chiari, T. Rajoafiarison, E. Rajeriarison, P. Bora and T. Razafindrabe; ZSM 226/2006 (ZCMV 2951), male, collected at Imaloka, Ranomafana National Park, south-eastern Madagascar, 21°14,527' S, 47°27,909' E; 1020 m a.s.l., on 23 February 2006 by Y. Chiari, P. Bora, T. Rajoafiarison, E. Rajeriarison, and T. Razafindrabe; ZSM 231/2006 (ZCMV

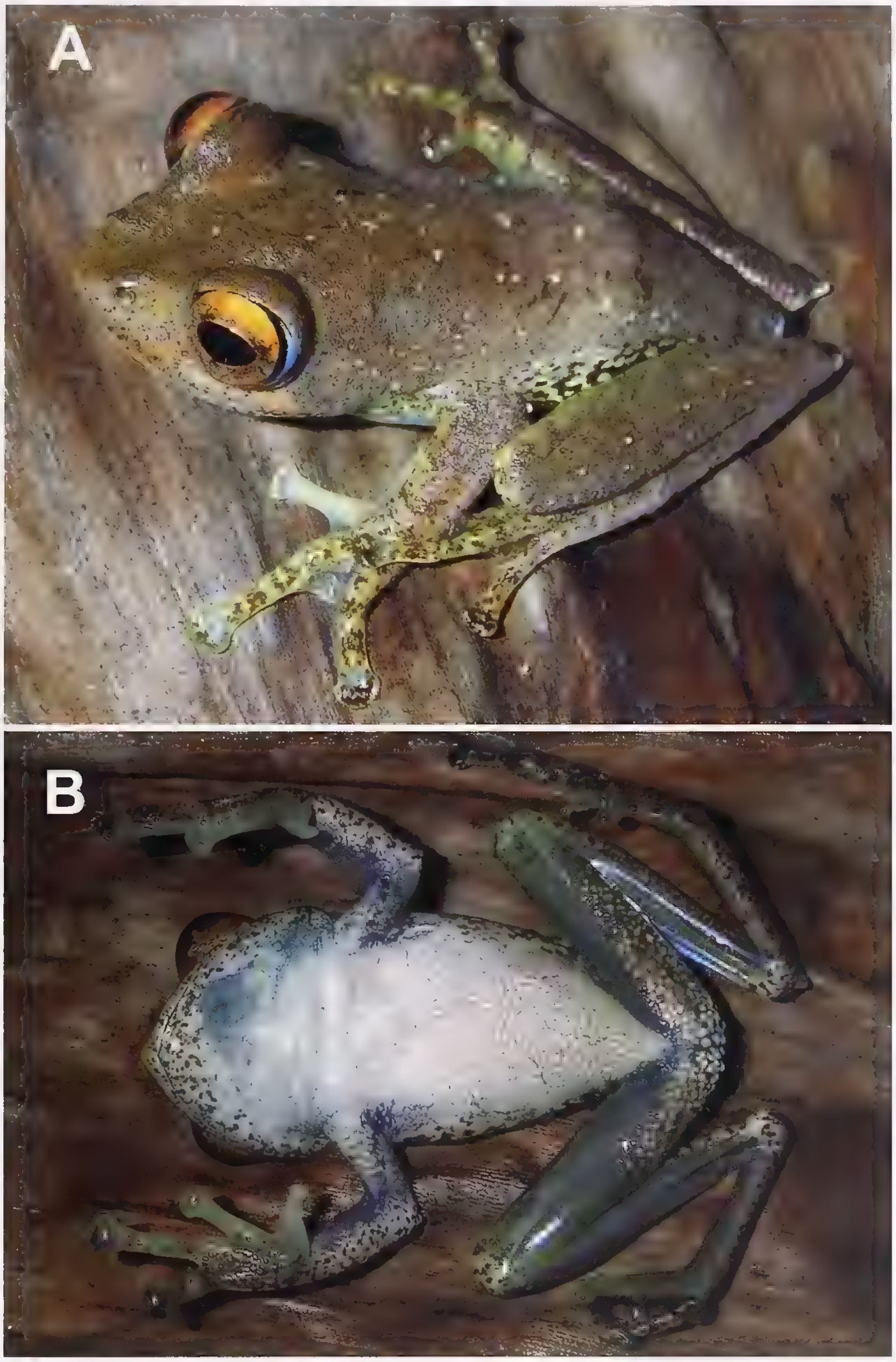

Fig. 5. Dorsolateral (A) and ventral (B) views of the male holotype of *Boophis quasiboehmei* sp. n. (ZSM 227/2006) in life.

3360), male, collected at Ranomena, 21°12,736' S, 47°26,010' E, Ranomafana National Park, south-eastern Madagascar, on 28 February 2006, M. Vences, Y. Chiari, T. Rajoafiarison, and E. Rajeriarison; ZSM 232/2006 (ZCMV 3374) from the Ranomafana region, perhaps collected at Ranomafanakely river but without precise collecting data; ZSM 2322/2007 (ZCMV 5948), male, collected at Sahamalaotra, Ranomafana National Park, south-eastern Madagascar, 21°14.113' S, 47°23.767' E, on 5 March 2007 by M. Vences, A. Strauß, R. D. Randrianiaina, and K. C. Wollenberg.

Diagnosis. Assigned to the genus *Boophis* based on the presence of an intercalary element between ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of nuptial pads and absence of femoral glands in males, and overall similarity to other *Boophis* species. Assigned to the *Boophis goudoti* group because of its brownish ground colour, presence of dermal flaps or tubercles on heels and elbows, presence of white tubercles ventrally of the cloacal opening, presence of a sharp canthus rostralis, absence of red skin colour, and molecular phylogenetic relationships.

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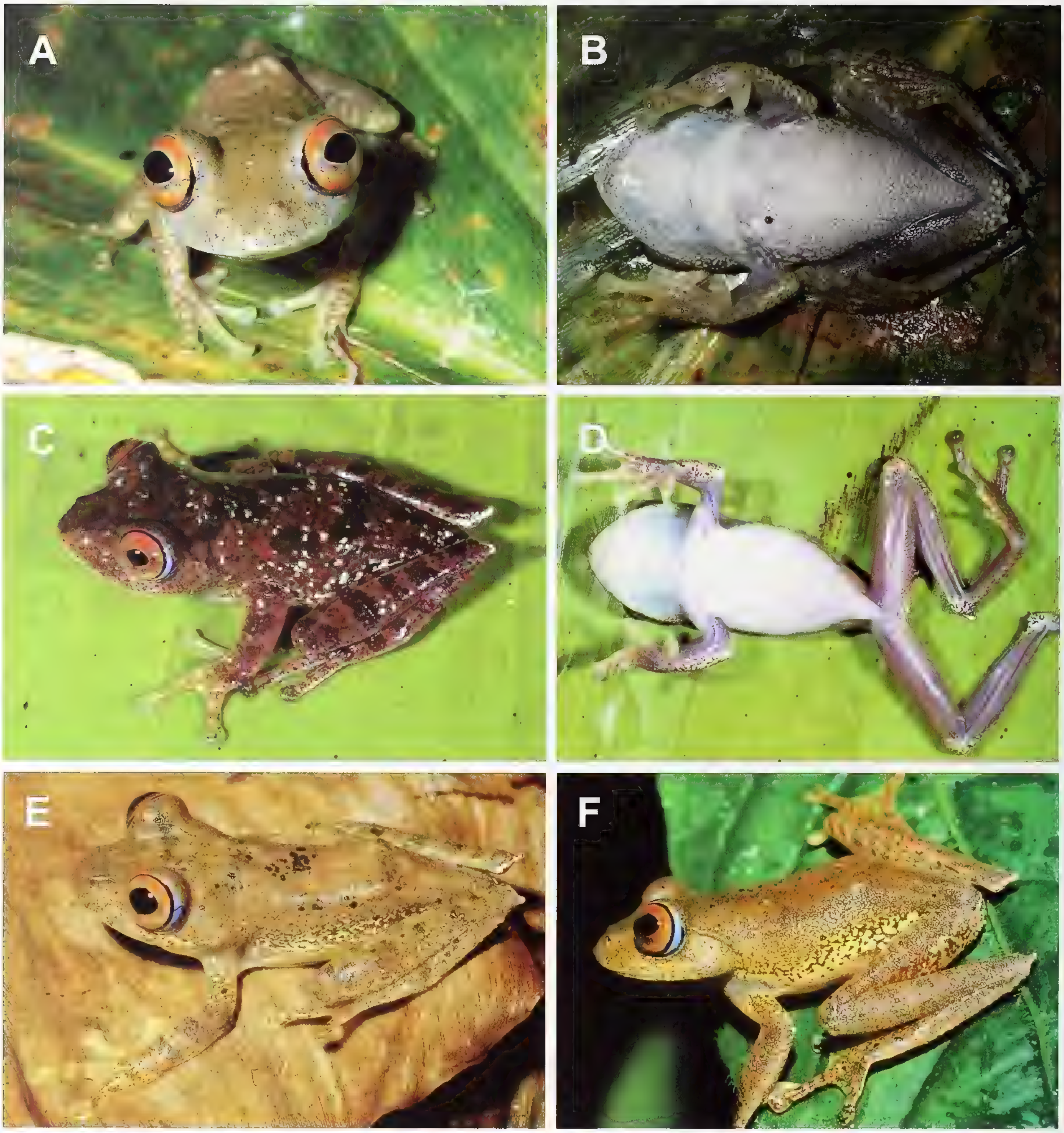

Fig. 6. Specimens of *Boophis quasiboehmei* sp. n. in life: (A) frontal and (B) ventral views of a male from Ambohitsara (field number ZCMV 5867); (C) dorsolateral and (D) ventral views of a male from Andohahela (deposited in UADBA); (E) male from Ranomafana (deposited in UADBA); (F) male paratype ZFMK 59882 from Ranomafana (photo by M. Burger).

Together with *B. boehmei*, the smallest species in the *Boophis goudoti* group characterized by a deviant oral morphology of the tadpole which is unknown from any other *Boophis* species. *Boophis quasiboehmei* sp. n. differs from all described species in the *B. goudoti* group by substantial genetic differentiation (> 6% pairwise divergence in a fragment of the 16S rRNA gene) and furthermore from *B. goudoti, B. obscurus, B. periegetes, B. madagascariensis, B. roseipalmatus, B. brachychir, B. entingae, B. rufioculis*, *B. burgeri*, *B. reticulatus*, *B. axelmeyeri*, and *B. spinophis* by smaller size (SVL of adult males 28–31 mm versus 31–82 mm) and bioacoustic differentiation (see Vences et al. 2006 for details). *B. quasiboehmei* sp. n. is most similar to *B. boehmei* and differs

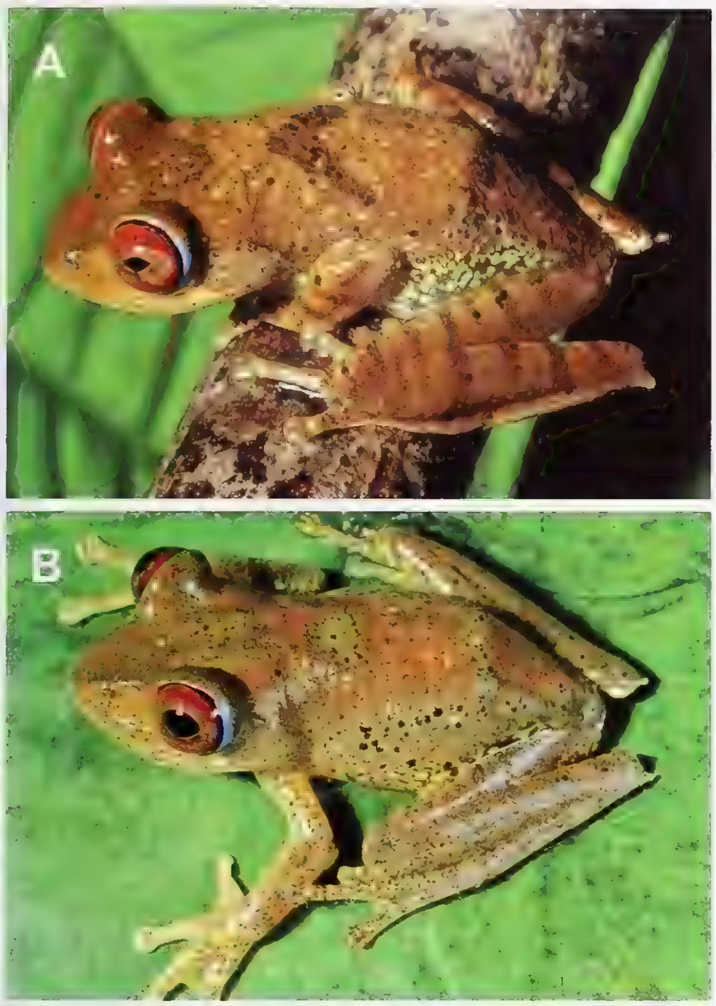

Fig. 7. Male specimens of *Boophis boehmei* from Andasibe in life: (A) paratype ZSM 563/1999 (originally ZFMK 53643); (B) paratype ZFMK 52637.

from this species by an orange (versus red) outer iris ring, by a very short third posterior keratodont row in the tadpole, consisting of only 0–15 keratodonts (versus 23–63 keratodonts in *B. boehmei*, see Randrianiaina et al. 2009b), and substantial genetic differentiation.

Description of holotype. Adult male in excellent state of preservation, muscles of right thigh removed as DNA tissue sample. SVL 26.7 mm. Body moderately slender; head slightly longer than wide, wider than body; snout pointed in dorsal view, obtuse to acuminate in lateral view; nostrils directed laterally, eqidistant to eye and to tip of snout; canthus rostralis sharp, straight in dorsal view from eye to nostril, slightly curved from nostril to tip of snout; loreal region slightly concave; eye large; tympanum distinct, rounded, TD 54% of ED; supratympanic fold narrow, prominent; vomerine odontophores distinct, well separated in two slightly elongated patches, positioned median between choanae; choanae medium-sized, rounded. Tongue distinctly bifid and free posteriorly. Arms moderately slender; a small pointed dermal appendage on elbow; subarticular tubercles single, round; inner palmar tubercle poorly recognizable; fingers poorly webbed and without lateral dermal fringes; webbing formula 1(–), 2i(–), 2e(1), 3i(1.5), 3e(1.5), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hind limbs slender; a pointed dermal appendage on heel; tibiotarsal articulation reaching widely beyond snout tip when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle medium-sized, distinct, elongated; no outer metatarsal tubercle; toes moderately webbed; webbing formula 1(0), 2i(1), 2e(0), 3i(1), 3e(0), 4i(2), 4e(2), 5(0.75); relative length of toes 1<2<3=5<4; toe discs enlarged. Skin smooth on dorsal surfaces, smooth on throat and chest, coarsely granular on belly, rather smooth on ventral surface of thighs, prominent scattered tubercles around cloaca. A worm-like parasite (possibly a nematode) apparently tried to escape when the frog was preserved and sticks in the left nostril.

Measurements (in mm): SVL 26.7, HW 10.6, HL 11.2, ED 3.7, END 2.3, NSD 2.3, NND 3.3, TD 2.0, TL 15.2, HAL 9.1, FOL 11.1, FOTL 20.8.

After almost four years in preservative, ground colour of upper surface of head, dorsum and limbs greyish brown, with few irregularly scattered and indistinct darker markings; supratympanic fold and tympanic region not distinctly coloured; upper lip creamy white; dorsal surfaces of thigh, shank, tarsus and external toe, as well as lower arm, hand and external finger with distinct dark brown crossbands; flanks brown with small pale white spots and dots, forming a reticulated pattern; several whitish dots below the cloaca, but no additional single white tubercles in the cloacal region; posterior surfaces of thighs greyish pale brown with beige reticulation on the proximal part, light brown without reticulations in the distal part; ventral surface creamy beige, with some pale greyish mottling along the lower jaw, the lower arms, hands and feet.

In life, ground colour of upper surface of head, dorsum and legs light brown (slightly darker on the head), with few irregularly scattered yellowish spots on the back and scattered dark dots on back and more densely on the lateral parts of the head; flanks with reticulated pattern of brown, yellow and white; upper surfaces of hands and feet mottled with brown and yellowish; outer edge of tarsus with thin white line and white tarsal tubercle, outer edge of lower arm with white tubercle; two irregular rows of white tubercles on shank; dorsal surfaces of limbs with moderately distinct brown crossbands; posterior surfaces of thighs white, numerous white tubercles around the cloaca and uniformly brown posteriorly. Throat, chest and venter creamy white; two irregular bluish spots on throat. Ventral surfaces of limbs only partially with whitish pigment, largest parts of thighs, shanks, hands and feet without white pigment. Outer iris almost uniformly bright orange, broadened above; inner iris ring brownish with some vessel-like brown reticulation; iris surrounded by a black ring; posterior iris periphery blue.

Variation. All paratypes were similar to the holotype in general morphology. For measurements, see Table 2. Male SVL ranged from 26.7–29.3 in the Ranomafana region, and was 30.8 mm in one specimen from Midongy. No females are known. Colouration was relatively constant in various localities of Ranomafana National Park, and in Ambohitsara (Fig. 6). The rather uniform orange eye colouration in life was typical for most specimens although at Andohahela (Fig. 6C) specimens tentatively assigned to this species had a more reddish eye colour.

Distribution. Besides different sites in (1) the Ranomafana region, the species is also known from (2) Tsitolaka forest near Ambohitsara, about 30 km from Ranomafana, and was tentatively identified from (3) Befotaka-Midongy Reserve (specimen ZSM 178/2006), and from (4) Andohahela National Park (Col Tanatana, 24°44’ S, 46°50’ E, 750 m a.s.l.). in the extreme southeast of Madagascar (GenBank accession number AY848529; specimen FGZC 236, deposited in UADBA).

Natural history. At Ranomafana National Park, *Boophis quasiboehmei* sp. n. was one of the most common species of frogs and its larvae occurred in 29 out of 30 streams surveyed for tadpoles (Randrianiaina et al. 2009b; Strauß et al. 2010). Adult specimens, however, were less commonly found, and in some areas occurred only in some densely clustered demes along small stretches of the streams. Males were observed calling at night from perch heights of 2–3 m from bushes and trees close to streams in primary as well as degraded rainforest.

Vocalization. Generally, calls of *Boophis quasiboehmei* sp. n. exhibit a characteristic structure, consisting of short to moderately long pulsatile notes. However, the pattern of emission of these notes is highly variable and mostly irregular. Sometimes, notes are combined to regular series (2–6 notes), with the initial note being longer than subsequent secondary notes. The calls emitted by the holotype (Fig. 8) and recorded on 26 February 2006 at Ambatovory have the main frequency distributed between 2100 and 3400 Hz, with additional frequency bands of lower amplitude at 5500–6000 Hz and 8100–8900 Hz. Numerical parameters for the holotype calls are as follows (range followed by mean ± standard deviation): duration of note series, 335–736 ms (519 ± 203; n = 3); number of notes per series, 3–6 (4.3 ± 1.5; n = 3); note duration (including initial notes within series), 66–79 ms (72.1 ± 4.6; n = 8), duration of secondary notes within series, 20–34 ms (24.9 ± 4.6; n = 8); pulses/note, 5–19 (12.6 ± 6.2; n = 15); inter-note intervals, 97–125 ms (109.9 ± 7.5; n = 10); dominant frequency, 2680–2963 Hz (2807 ± 86; n = 10).

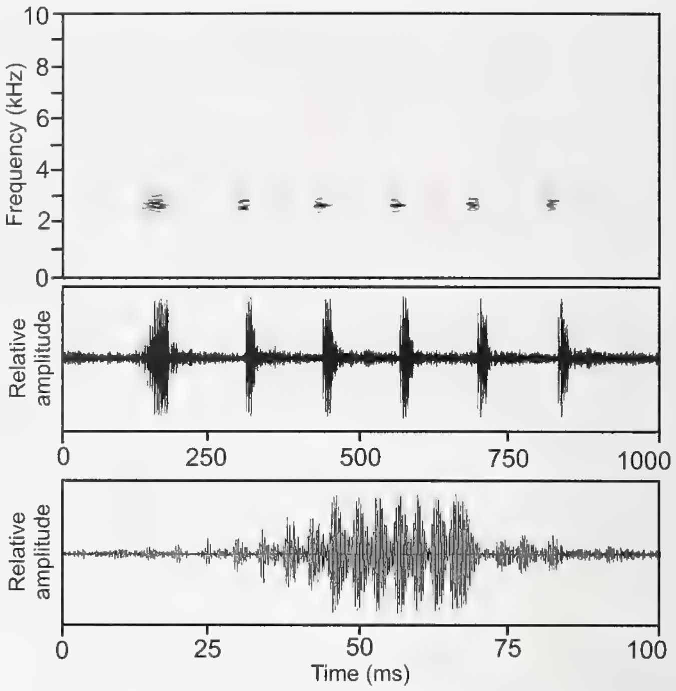

Fig. 8. Spectrogram, corresponding waveform, and expanded waveform (bottom) of the initial note of a regular note series emitted by the holotype of *Boophis quasiboehmei* sp. n. Recording obtained on 26 February 2006 at Ambatovory, Ranomafana National Park.

A short sequence with three notes recorded on 1 March 1996 at Ranomafana (Vences et al. 2006, CD 1, track 66) has the following parameters: duration of note series, 373 ms, notes/series, 3; note duration, 18–58 ms; pulses/note, 5–12; inter-note intervals, 139–142 ms; dominant frequency, 2550–2637 Hz.

Calls of *B. quasiboehmei* sp. n. from Ambohitsara recorded on 3 March 2007 generally agree in structure with those emitted by the holotype, although they have shorter note duration and more variable, distinctly longer inter-note intervals. Numerical parameters are as follows: duration of note series, 527 ms (n = 1); number of notes per series, 6 (n = 1); note duration (including initial notes within series), 22–47 ms (35.2 ± 7.3; n = 13); pulses/note, 4–12 (7.9 ± 2.5; n = 18); inter-note intervals, 475–942 ms (724.4 ± 138.8; n = 16); dominant frequency, 2293–2572 Hz (2465 ± 90; n = 9).

Comparative call data. The morphologically most similar species, *Boophis boehmei*, has an almost identical call compared to that of *B. quasiboehmei* sp. n. A re-analysis of calls of *B. boehmei* from Andasibe (type locality) recorded on 12 January 1992 at 23°C (Fig. 9) revealed the following parameters: duration of note series, 455–530 ms

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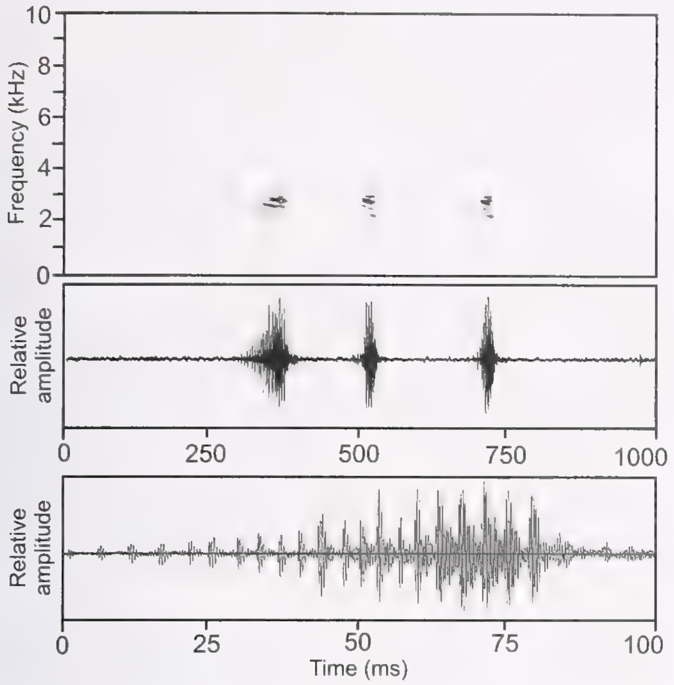

Fig. 9. Spectrogram, corresponding waveform, and expanded waveform (bottom) of the initial note of a regular note series emitted by *Boophis boehmei*. Recording obtained on 12 January 1992 at Andasibe (air temperature 23°C).

(n = 2); number of notes per series, 3–4 (n = 2); note duration, 27–106 ms (62.6 ± 23.0; n = 11); pulses/note, 10–24 (15.7 ± 4.8; n = 9); inter-note intervals, 93–157 ms (125.0 ± 29.6; n =5); dominant frequency, 2640–3177 Hz (2835 ± 165.6; n = 8).

A second recording from the type locality of *B. boehmei* recorded on 7 December 2001 at 24.8°C (Vences et al. 2006, CD 1, track 64) differs from the one described above by longer inter-note intervals. Numerical parameters are as follows: note duration, 34–98 ms (62.7 ± 19.7; n = 18); pulses/note, 13–23 (16.7 ± 3.6; n = 11); inter-note intervals, 591–1070 ms (766.1 ± 210.0; n =7); dominant frequency, 2360–2980 Hz (2760 ± 198; n = 12). In this recording, a single regular series composed of 6 notes is present, exhibiting note durations of 34–44 ms and internote intervals within the series of 61–85 ms.

A call recording of *B. boehmei* from Ankeniheny recorded on 20 March 1994 at 22°C air temperature showed note duration of 16–61 ms, inter-note intervals of 162–164 ms and a dominant frequency of 2500–2800 Hz.

In conclusion, there are no temporal or spectral call characters that distinguish *B. boehmei* from *B. quasiboehmei* sp. n. (see above).

Etymology. The specific epithet is a combination of the Latin word 'quasi', meaning 'almost', and a patronym for Wolfgang Böhme (ZFMK). It refers to the impressively cryptic morphological and bioacoustic similarity of the new species to *Boophis boehmei*.

DISCUSSION

The initial detection of a probable species status of *Boophis quasiboehmei* sp. n. was based on its large divergence in a single marker of mitochondrial DNA. Due to the extent of this divergence (>6% to all described species), Vieites et al. (2009) deviated slightly from their usual rationale and listed this species as confirmed candidate species, despite the lack of concordant indications by independent taxonomic characters. Although the work protocol of integrative taxonomy proposed by Padial et al. (2010) would allow for the description of species based on single characters if these are deemed to be sufficiently indicative of the existence of independent evolutionary lineages, we do not recommend this procedure. Instead, we only decided to formally describe *B. quasiboehmei* sp. n. as new species once that independent and congruent evidence of various taxonomic characters had accumulated, even if those were subtle at first view: (1) a weak and not fully constant difference in adult eye colouration, (2) a slight tendency of morphometric differentiation detectable only by multivariate techniques, (3) a constant difference in tadpole morphology, and (4) concordance between three independent molecular markers (two nuclear and one mitochondrial). The molecular concordance alone would be sufficient for species recognition under the genealogical concordance method of phylogenetic species recognition, GCPSR (Avise & Ball 1990), but the further strict concordance with one morphological character (tadpole labial keratodonts) provides a more convincing evidence, especially because it is based on large series of individuals (Randrianiaina et al. 2009a, b). We are therefore convinced that *Boophis quasiboehmei* sp. n. and *B. boehmei* are to be considered as distinct species under an evolutionary or general lineage species concept (de Queiroz 2007).

Among the various mechanisms of species diversification discussed for Madagascar (Vences et al. 2009), two (the watershed and the river barrier mechanism) might apply to the species pair *B. boehmei* and *B. quasiboehmei* sp. n. that occur in two different neighbouring centres of endemism (CE2 and CE3) as defined by Wilmé et al. (2006), and because these two CEs are divided by the Mangoro river that has been invoked as an important river barrier in eastern Madagascar (see Vences et al. 2009). Discerning between these hypotheses is difficult, but both are contradicted by the fact that *B. quasiboehmei* sp. n. also occurs in Andohahela, which is in a different CE (CE5) and separated by a further large river barrier (the Mananara river). Also, the fact that numerous other red-eyed

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treefrog species and candidate species have been already identified from eastern Madagascar (see Vieites et al. 2009: *B. axelmeyeri, B. rufioculis, B.* sp. 8, *B.* sp. 40, *B.* sp. 41), several of which appear to be microendemic to small areas while others might be more widespread, indicates a more complex situation. Only a more comprehensive study of this group, with assessments of the status of all candidate species and their phylogenetic relationships, and a more detailed analysis of their distribution, will significantly contribute to the understanding of the diversification mechanisms that may have lead to this surprising morphological cryptic diversity. However, the fact that the phylogenetic position of *B. boehmei* and *B. quasiboehmei* is unclarified should not be interpreted as casting doubts on the species status of *B. quasiboehmei* since this new species is differentiated from topotypical *B. boehmei* by a high genetic differentiation and tadpole mouthparts, and from all other nominal species in the *B. goudoti* group by a high genetic differentiation, tadpole mouthparts, adult morphology, and advertisement calls. However, clarifying the phylogenetic relationships of all species and candidate species will be important to understand the status of the various UCS and CCS in the group and to be able to provide formal descriptions of those for which the data will confirm the status as distinct species. Additional data still missing at this time are on tadpole morphology of the populations from Andohahela, Midongy, Sahafina and Mahasoa that herein we have assigned in a preliminary way to *B. quasiboehmei* (Andohahela, Midongy) or different candidate species (Sahafina, Mahasoa).

At Ranomafana National Park, *Boophis quasiboehmei* sp. n. was commonly encountered at least in its tadpole stage, and its occurrence was confirmed at Andohahela National Park and tentatively in Befotaka-Midongy National Park. Although we never observed the species in secondary vegetation formations, it appears to be tolerant to some degree of rainforest degradation. The relatively large distribution area (from Ranomafana to Andohahela), its occurrence in at least two protected areas and large area of occupancy at least in the Ranomafana area lead us to propose an IUCN red list status of Least Concern for this newly described species (compare Andreone et al. 2005, 2008).

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A new species of *Pachydactylus* (Squamata: Gekkonidae) from the Otavi Highlands of northern Namibia

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Abstract. A new species of the "northwestern clade" of *Pachydactylus* is described from the Otavi Highlands of northeastern Namibia. It is distinguishable from all other members of this clade and from the superficially similar members of the *Pachydactylus serval/weberi* group on the basis of its inclusion of the rostral in the nostril rim, the possession of a maximum of only four undivided scansors beneath the digits of the pes, is 16 rows of strongly keeled, rounded, juxtaposed dorsal trunk tubercles, its projecting, keeled, lanceolate caudal tubercles, and its complex dorsal trunk patterning. Its probable closest relative is *P. otaviensis*, also form the Otavi Highlands. These are the only known endemic reptiles from this dolomitic area and their existence points both to an unappreciated area of diversity and endemism in northeastern Namibia and to the need for additional herpetological work in even well-known parts of the country.

Key words. Gekkonidae, *Pachydactylus*, Namibia, new species.

INTRODUCTION

Pachydactylus Wiegmann, 1834 is the most species-rich genus of geckos in southern Africa, with more than 50 species currently recognized (Bauer & Lamb 2005; Bauer et al. 2006a, 2006b; Branch et al. 2010). Although all parts of the subcontinent are inhabited by members of this group, the arid zones of Namibia the adjacent portions of the Northern Cape Province of South Africa have the highest diversity. A minimum of 35 species of *Pachydactylus* occur in the Republic of Namibia alone, the majority of which are endemic (Branch 1998; Bauer et al. 2002, 2006a; Branch et al. 2010). Most of these fall into one of two species-rich clades that have been previously identified: the *Pachydactylus serval/weberi* group and the "northwestern clade" of *Pachydactylus* (*sensu* Bauer & Lamb 2005). Most species in both clades are relatively small-bodied, rupicolous species. Most members of the *P. serval/weberi* group are restricted to southern Namibia and the Northern Cape, with the greatest richness along the lower Orange River Valley and in the Karasberg Mountains, where up to five members of the group occur sympatrically. However, five members assigned to the group have been found north of 21°S latitude: *P. fasciatus* Boulenger, 1888 – widely distributed in northwestern Namibia east of the Namib and north of the Swakop River, *P. waterbergensis* Bauer & Lamb, 2003 – endemic to the immediate vicinity of the Waterberg Plateau. *P. tsodiloensis* Haacke, 1966 – in the Tsodilo Hills of northwestern Botswana, and *P. otaviensis* Bauer, Lamb & Branch, 2006 and an undescribed species ('*Pachydactylus* sp. 2', Bauer et al. 2006a) – both from the Otavi Highlands (Otaviberge) of northeastern Namibia. Bauer & Lamb (2005) and Bauer et al. (2006a) used molecular phylogenetic data to confirm that the first three of these species comprise a monophyletic group that is sister to the rest of the *P. serval/weberi* group. However, recent multi-gene phylogenetic analyses incorporating all but one of the recognized species of *Pachydactylus* (Heinicke, Jackman & Bauer, unpublished) have demonstrated that *P. otaviensis* is not a member of the *P. serval/weberi* clade (these phylogenetic results will be presented in their entirety elsewhere), but rather part of the "northwestern clade", which otherwise comprises ten morphologically diverse species that are widely distributed in Namibia and southern Angola, with a single species, *P. punctatus* Peters, 1854, extending southwards into South Africa and east to the Indian Ocean coast of Mozambique (Bauer & Branch 1995).

Excluding *P. punctatus*, *P. otaviensis* has the easternmost distribution of any member of the "northwestern clade", being known only from the farms Uithoek and Varianto, both in the Tsumeb District, Oshikoto Region in the eastern Otavi Highlands (quarter degree square 1917Bc; Fig. 1). A second species from the Otavi Highlands was sig-

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Table 1. Mensural and labial scale data for the type series of *Pachydactylus boehmei* sp.n. Abbreviations as in Materials and Methods, all measurements in mm.

	Holotype	Paratypes			
	MCZ R184884	MCZ R184880	MCZ R184881	MCZ R184882	MCZ R184883
Sex	female	female	female	male	female
SVL	44.4	43.21	44.0	35.4	34.8
ForeaL	6.6	6.8	6.6	5.4	4.7
CrusL	7.9	7.9	8.6	5.5	5.9
TailL (total)	44.5	6.9	39.0	35.8	30.3
TailL (regen.)	–	BR	33.4	–	21.6
TailW	4,8	4.7	4.7	3.9	3.5
TrunkL	21.0	18.8	19.0	15.6	13.8
HeadL	13.7	14.1	13.0	11.5	12.0
HeadW	8.3	8.3	9.0	6.9	7.2
HeadD	5.0	5.3	5.3	3.8	4.0
OrbD	3.5	3.8	3.8	2.8	3.3
EyeEar	3.4	3.7	3.2	2.9	2.5
SnEye	4.9	5.0	4.7	4.2	4.2
NarEye	3.7	3.9	3.6	2.9	3.0
Interorb	4.4	4.3	3.9	3.6	3.0
EarL	1.0	0.9	1.0	0.7	0.7
Internar	1.4	1.1	1.3	1.0	1.2
Supralab. (L/R)	10/9	11/10	10/10	9/9	10/10
Infralab. (L/R)	7/7	8/8	7/8	8/8	9/8

naled by Bauer et al. (2006a) as "*Pachydactylus* sp. 2", but was not described as it was known only from one juvenile and one hatchling, making meaningful comparisons with other species difficult. However, Bauer et al. (2006a) noted that it exhibited some features shared with the *P. weberi* complex *sensu stricto* and others with the *P. serval* complex, and that it possessed a unique and diagnostic juvenile color pattern. Subsequent field work on the Farm Uisib has yielded a series of adult specimens of this species, permitting its description. Ongoing molecular phylogenetic work verifies that it too is, in fact, correctly assigned to the "northwestern clade" of *Pachydactlyus*.

MATERIALS AND METHODS

The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.1 mm) as per Bauer et al. (2006a): snout-vent length (SVL; from tip of snout to vent), crus length (CrusL; from base of heel to knee); tail length (TailL; from vent to tip of unregenerated tail), tail width (TailW; measured at base of tail); axilla to groin length (TrunkL); head length (HeadL; distance retroarticular process of the jaw and snout-tip), head width (HeadW; measured at angle of jaws), head depth (HeadD; maximum height of head, from occiput to throat), ear length (EarL; longest dimension of ear); forearm length (ForeaL; from base of palm to elbow); orbital diameter (OrbD), nostril to eye distance (NarEye; distance between anteriormost point of eye and nostril), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), eye to ear distance (EyeEar; distance from anterior edge of ear opening to posterior corner of eye), and interorbital distance (Interorb; shortest distance between left and right superciliary scale rows).

Scale counts and external observations of morphology were made using a Nikon SMZ-1000 dissecting microscope. Comparisons were made with museum material (see Appendix) representing all species in the *Pachydactylus serval/weberi* group and the "northwestern clade" of *Pachydactylus* (*sensu* Bauer & Lamb 2005; Bauer et al. 2006a). Standard codes for museum collections follow Leviton et al. (1985) except as noted (*): California Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ), National Museum of Namibia, Windhoek (NMN*), Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main (SMF), South African Museum, Cape Town (SAM), Transvaal Museum, Pretoria (TM), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK).

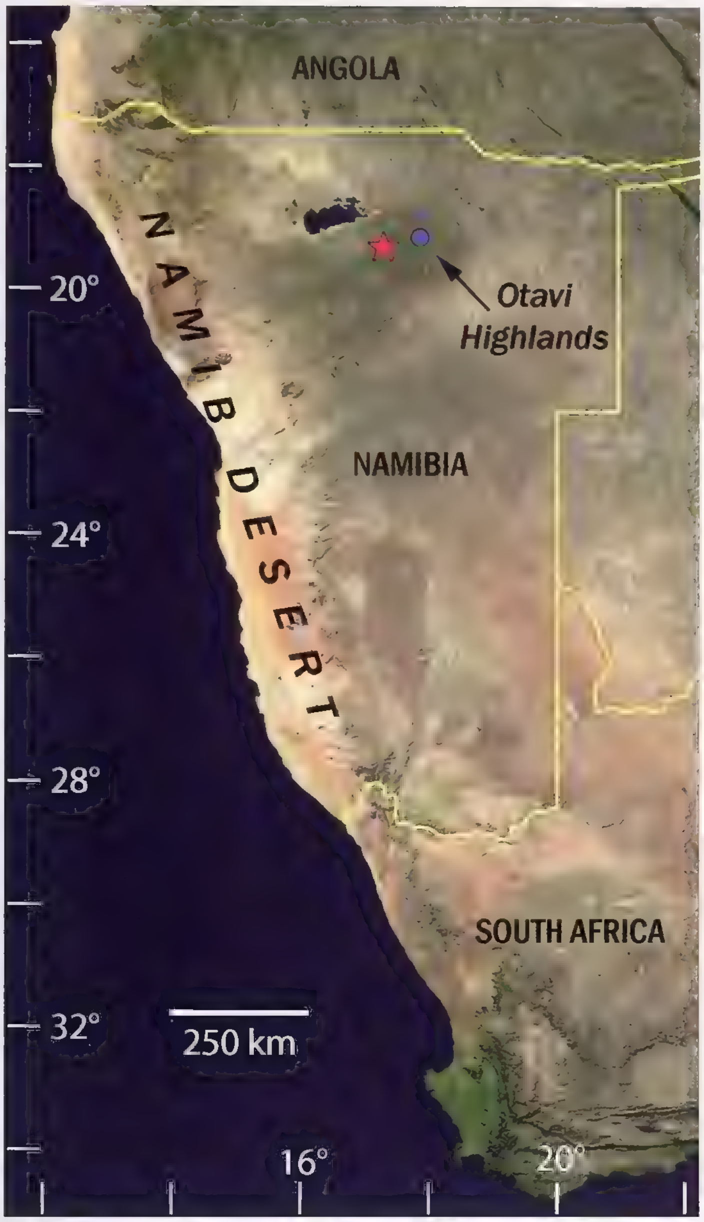

Fig. 1. Map of Namibia and surrounding countries illustrating the type locality of *Pachydactylus boehmei* sp. n. (red star) and of the related *P. otaviensis* (blue circle) in the Otavi Highlands of northeastern Namibia. Satellite image from NASA MODIS sensor (available at http://visibleearth.nasa.gov).

RESULTS

Pachydactylus boehmei sp. n.

Pachydactylus sp. 2 Bauer, Lamb & Branch (Bauer et al. 2006a: 684)

Holotype. MCZ R184884 (Figs 2–3): adult male; Namibia, Otjozondjupa Region, Grootfontein District, Farm Uisib, 19°33'06"S, 17°14'11"E, 1400 m a.s.l. coll. A.M. Bauer, J. Marais, T. Jackman, and W.R. Branch, 15 September 2006.

Paratypes. MCZ R184880–81 (adult females), 184883 (subadult/adult female), MCZ R184882 (subadult/adult male), same data as holotype.

Additional material. TM 84999, 85005; Namibia, Otjozondjupa Region, Grootfontein District, Farm Uisib (19°33'08"S, 17°14'07"E).

Diagnosis. Snout-vent length to at least 44.4 mm. A moderate-sized *Pachydactylus* with a depressed body form. Trunk with 16 rows of enlarged, keeled tubercles, grading into prominent conical scales on flanks (Figs 2–4). Orbital diameter as great as eye-ear distance. Rostral participating in nostril rim. Dorsal surface of thighs and shanks covered by enlarged conical to keeled scales. Tail with keeled lanceolate tubercles restricted to one scale row per tail segment. Dorsal pattern with an occipital-nuchal loop, a "V"-shaped band on posterior of neck, a transverse bar anterior to hindlimb insertion, and a series of oval markings or fusions thereof on the trunk (Figs 2–5).

Among its congeners *P. boehmei* sp n. is superficially similar to some members of the *P. weberi* group, but can be distinguished from these by its inclusion of the rostral in the nostril rim and the possession of a maximum of only four undivided scansors beneath the digits of the pes (versus at least five on some digits). Among other members of the "northwestern clade" of *Pachydactylus* it may be differentiated from *P. bicolor* Hewitt, 1926, *P. punctatus*, *P. scherzi* Mertens, 1954, and *P. caraculicus* FitzSimons, 1959 by its tuberculate (versus atuberculate) dorsum, from *P. angolensis* Loveridge, 1944 by its inclusion of the rostral and first supralabial in the nostril border (versus both excluded), from *P. oreophilus* McLachlan & Spence, 1967 by its smaller size (maximum SVL < 45 mm versus 57 mm), and lower number of subdigital lamellae (4 versus 5–6 undivided lamellae), from *P. gaiasensis* Steyn & Mitchell, 1967 by its smaller size (maximum SVL < 45 mm versus 68 mm), lower number of subdigital lamellae (4 versus 5–7 undivided lamellae), longer tail (slightly longer than SVL versus less than SVL), and lack of a vertebral stripe, from *P. sansteynae* Steyn & Mitchell, 1967 by its much larger dorsal tubercles (4–10 times larger than other dorsal scales versus less than twice size of dorsal granules) and presence (versus absence) of tubercles on the parietal region, from *P. parascutatus* Bauer, Lamb & Branch, 2002 by its larger size (to 44.4 mm versus < 40 mm SVL) and presence of a pale dorsal collar (versus no collar), and from *P. scutatus* Hewitt, 1927 by is juxtaposed (versus imbricating) keeled dorsal scales, enlarged conical (versus small and granular) flank scales, projecting lanceolate (versus flattened and rounded to oval) caudal tubercles, and its complex dorsal trunk patterning (versus patternless or with small, scattered dark markings. *Pachydactylus boehmei* sp n. is most similar to the geographically proximal *P. otaviensis*, but may be distinguished from this form by its inclusion (versus exclusion) of the rostral in the nostril rim, the presence of 4 (versus 5) lamellae beneath digit IV of the pes, 16 (versus 18) longitudi-

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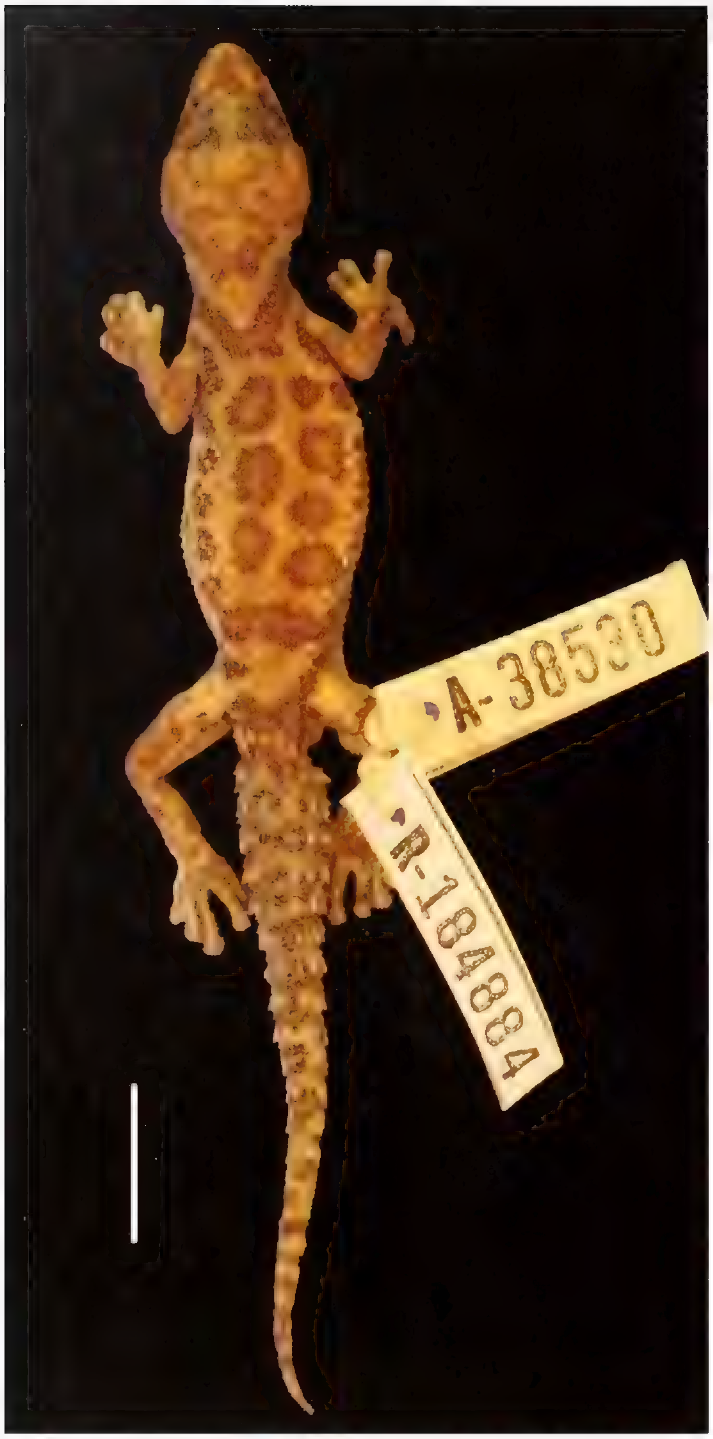

Fig. 2. Holotype of *Pachydactylus boehmei* sp. n., MCZ R184884. Scale bar = 10 mm.

nal rows of keeled dorsal tubercles, and differences in color pattern.

Description of holotype. Adult female. Snout-vent length (SVL) 44.4 mm. Body relatively depressed, elongate (TrunkL/SVL ratio 0.46). Head elongate, large (HeadL/SVL ratio 0.31), relatively narrow (HeadW/HeadL ratio 0.61), depressed (HeadH/HeadL ratio 0.36), distinct from neck. Lores inflated; interorbital region flat. Snout short (SnEye/HeadL ratio 0.36, longer than eye diameter (OrbD/SnEye ratio 0.71); scales on snout enlarged, smooth, slightly domed, roughly hexagonal; scales on snout much larger than those of interorbital region and parietal table. Eye moderately large (OrbD/HeadL ratio 0.25); orbits without extra-brillar fringes; posterior superciliary scales bearing five small spines; pupil vertical, with crenelated margins. Ear opening oval, small (EarL/HeadL ratio 0.07), round; eye to ear distance approximately equal to diameter of eyes (Eye-Ear/OrbD ratio 0.97). Rostral approximately 50% as deep (0.9 mm) as wide (1.9); no rostral groove; contacted by two enlarged supranasals and first supralabials; nostrils oval, each surrounded by two postnasals, one supranasal, first supralabial, and rostral; supranasals in broad contact; dorsal postnasals separated by two granules from one another; nostril rims weakly inflated; 1–2 rows of scales separate orbit from supralabials; mental rectangular, only slightly wider anteriorly than posteriorly, approximately 1.6 times deeper (1.8 mm) than wide (1.1 mm); no enlarged postmentals or chin shields. Enlarged supralabials to angle of jaws 9(R)–10(L), 8 to mid-orbit, several granular scales along labial margin to rictus; enlarged infralabials 7; interorbital scale rows between superciliary scale rows (at midpoint of orbit) 30, 8 across narrowest point of frontal bone.

Enlarged conical tubercles present from posterior border of orbit and occiput posteriorly; dorsal trunk tubercles large (4–10 times size of adjacent scales), rounded, with a strongly developed median keel, forming approximately 16 longitudinal rows; tubercles largest on dorsolateral surfaces of trunk, smaller along vertebral midline, and grading into enlarged conical scales on flanks; each enlarged tubercle surrounded by rosette of smaller pyramidal scales, some also keeled, larger keeled tubercles typically separated from one another by a single smaller scale; ventral scales flattened, subimbricate, becoming somewhat larger posteriorly, approximately 40 between lowest tubercular rows at midbody; non-tuberculate scales on dorsum at midbody similar in size to those on ventrum at same level; gular granules less than one half size of ventral scales of chest, increasing abruptly in size on throat. No precloacal or femoral pores. Scales on palm, sole, and ventral surface of forelimb small, smooth, granular, juxtaposed; scales on ventral aspect of hindlimbs smooth, juxtaposed to subimbricate; scales on dorsal aspect of forelimb heterogeneous, with midsized conical to keeled tubercles intermixed with smaller granular to conical scales; scales on dorsum of thigh and crus greatly enlarged, conical and keeled, in contact with each other or narrowly separated by much smaller interscales.

Forelimbs moderately short, stout; forearm short (ForeaL/SVL ratio 0.15); hindlimbs relatively short, tibia moderately short (CrusL/SVL ratio 0.18); digits relatively short, claws minute, stylet-like, visible only with difficul-

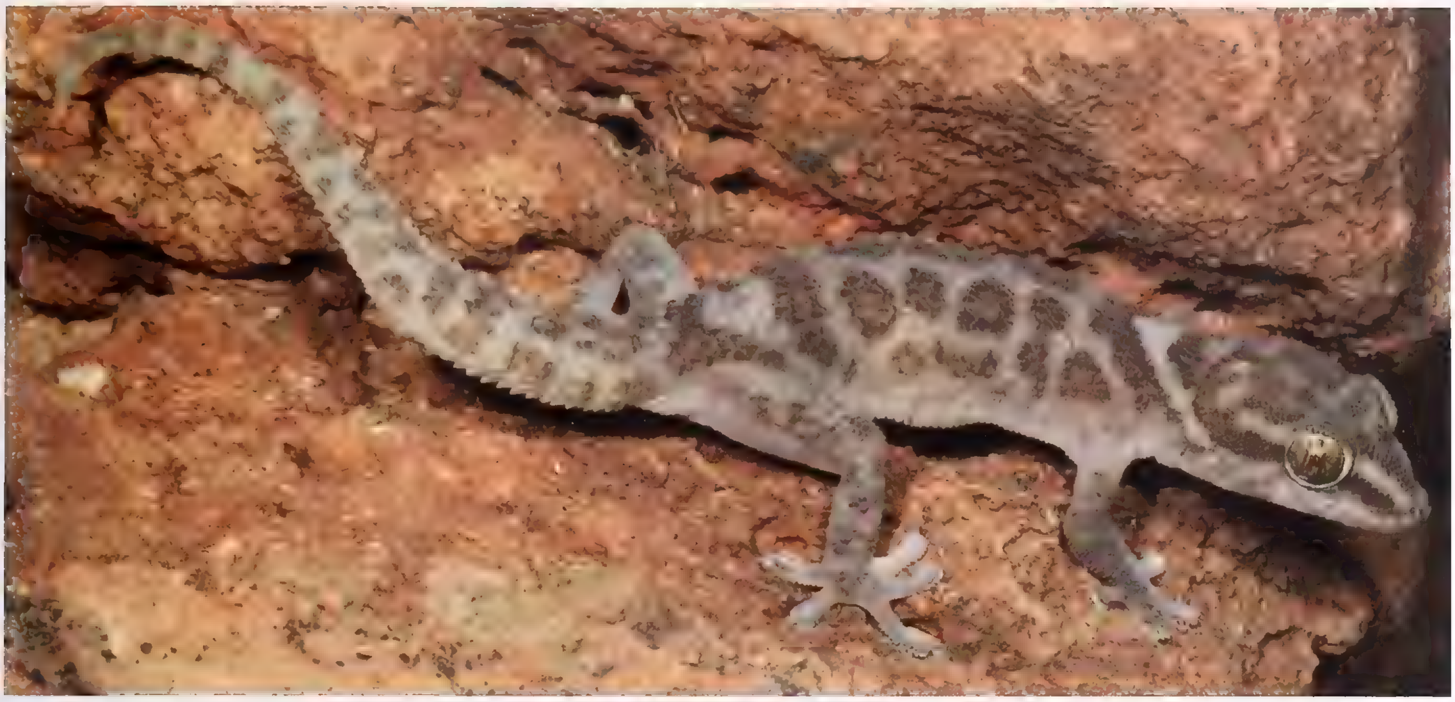

Fig. 3. Life photo of holotype of *Pachydactylus boehmei* sp. n. Photo by Johan Marais.

ty on some digits of the pes; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.5 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III > IV > II > V > I; (pes): IV > III > V > II > I. Subdigital scansors, exclusive of divided distalmost scansor (manus): I (4), II (4), III (4), IV (4), V (4); (pes) I (4), II (4), III (4), IV (4), V (4).

Tail sub-cylindrical, clearly depressed; original tail approximately snout-vent length (TailL/SVL ratio 1.00); tail constricted basally, then expanded before tapering towards tip, distinctly segmented; each segment with 5 rows of scales dorsally and 3 ventrally, dorsal caudal , tail segment; caudal tubercles heterogeneous, medial tubercles more-or-less recumbent, lateral tubercles projecting, up to 8 keeled tubercles per row basally, decreasing to 4 on distal caudal segments; subcaudal scales smooth, imbricating, oval to rectangular; no enlarged postcloacal spurs on side of tailbase.

Coloration. In preservative (Fig. 2): Ground color of dorsum straw to yellowish brown with mid-brown markings. A broad “V”-shaped nape band and a transverse band anterior to hindlimb insertion. Trunk bearing a series if irregular oval markings, darker on their edges than at their centers, 3 (left) and 4 (right) markings in paravertebral position, 6 on upper left flank, last fused with transverse band, 2 on upper right flank followed by an irregular longitudinal marking representing the fusion of several oval markings. An additional pair of small dark markings at anterior face of hindlimb insertion and an additional crossband on dorsum of posterior sacrum.

Head with a pale stripe from nostril to anterodorsal rim of orbit. Dark stripe along loreal region to mid-anterior of orbit, continuing from midposterior of orbit, above ear, to meet contralateral stripe to form a complete loop between the occiput and nape. Crown mottled, a triangular brown marking with apex at supranasals scales extending back to anterodorsal orbital rim. Labial scales pale with diffuse speckling; grayish vertical markings on lateral edges of rostral.

Limbs mottled with irregular markings. Tail with alternating irregular bands of grayish-brown and mid-brown, 20 dark bands including tail tip; most caudal tubercles cream to beige. Body venter beige, soles and palms grayish, tail venter grayish-brown with irregular darker gray-brown markings scattered along length of tail.

In life (Fig. 3): Background color of dorsum a pale pinkish-gray. Labial scales, canthal stripe, and nape whitish. Dark markings yellowish-to mid brown, darkest on head and occiput. Venter white.

Variation. Variation in mensural characters of the holotype and paratypes are presented in Table 1. All paratypes share with the holotype the same number of longitudinal rows of dorsal tubercles, number of subdigital lamellae, and configuration of the scales of the nasal region. Labial scale numbers varied across the type series and are also presented in Table 1. The male paratype, MCZ R184882 has prominent precloacal spurs (Fig. 4A), each bearing two rows of enlarged, compressed, dorsally-directed scales. Those of the dorsal row (5 scales on both sides) larger than those of ventral row (5 scales left, 6 scales

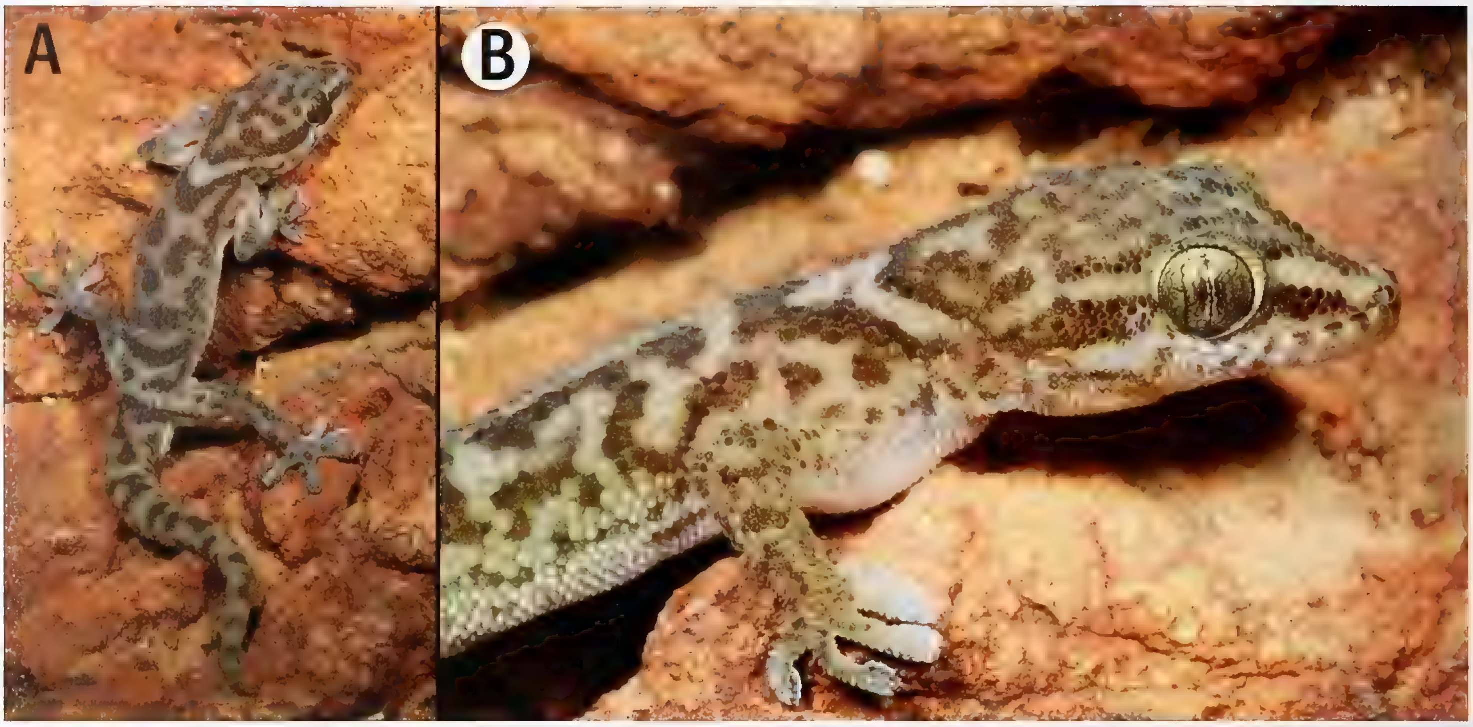

Fig. 4. Life photos of paratypes of *P. boehmei* sp. n. (A) MCZ R184882, male – note the raised precloacal spur visible lateral to the tail base. (B) MCZ R184880, female – note the transition from rounded, keeled dorsal tubercles to enlarged conical flank scales. Photos by Johan Marais.

right). Color pattern variable amongst paratypes (Figs 4–5). Dark occipital and nape bands thinner in MCZ R184880, R184882 than in holotype. Dorsal oval patterns largely replaced by coalescent blotches and lines except in MCZ R184881. Dorsal pattern weakly contrasting in MCZ R184883.

Etymology. Named for Prof. Dr. Wolfgang Böhme (born 21 November 1944), my longtime friend and colleague and a leading contributor to African herpetology. It is a privilege to apply this patronym to a species of one of the continent's dominant genera on the occasion of his nominal retirement from his position at the Museum Alexander Koenig. The epithet is formed in the masculine genitive.

Distribution. The species is known only from Farm Uisib in the Grootfontein District of northeastern Namibia (Fig. 1). This lies in the western portion of the Otaviberge or Otavi Highlands, 15 km northwest of the town of Otavi. The distribution of *P. boehmei* sp n. in the region is unknown and the closely related *P. otaviensis* occurs only 50 km to the northeast. These two geckos are relatively isolated from other members of the "northwestern clade" of *Pachydactylus* except the ubiquitous *P. punctatus*; the nearest known localities for *P. bicolor* and *P. scutatus* being more than 200 km distant. Other rock-dwelling congeners in other clades are also quite remote, with *P. waterbergensis* approximately 125 km to the south and *P. tsodiloensis* almost 400 km to the north-northeast. The Otavi Highlands as a whole has been poorly explored herpetologically and may harbor other isolated populations and/or endemic species of lizards. A number of endemic invertebrates and fish are already known from the Otavi-Tsumeb-Grootfontein area (Barnard et al. 1998).

Natural history. The area where *P. boehmei* sp n. occurs is characterized as mountain savanna and karstveld (Giess 1971). The type series was collected in broadleaf savanna on rocky dolomite hills (Fig. 6). Specimens collected by the author and colleagues were moving on rock faces or were found in large crevices or cracks between 22:30 and 00:30. The two Transvaal Museum specimens (see Additional material) referred to this species were collected in the course of searching for scorpions (E. Scott & L. Prendini, pers. comm.). Barnards Namib day gecko, *Rhoptropus barnardi* Hewitt, 1926, was also collected at Farm Uisib, which is one of the easternmost localities for any member of its genus. Other species observed at the type locality were the widespread *Chondrodactylus turneri* (Gray, 1864), *Trachylepis sulcata* (Peters, 1867), and *T. punctulata* (Bocage, 1872). *Lygodactylus capensis* (Smith, 1849) was collected at the nearby Uisib farmhouse (19º33'11"S, 17º13'00"E).

Two enlarged eggs are visible through the ventral body wall of the holotype collected in mid-September, suggesting spring breeding and hatching late in the year, corresponding to the rainy season. Trombiculid mites were found on the specimens, most notably in between the

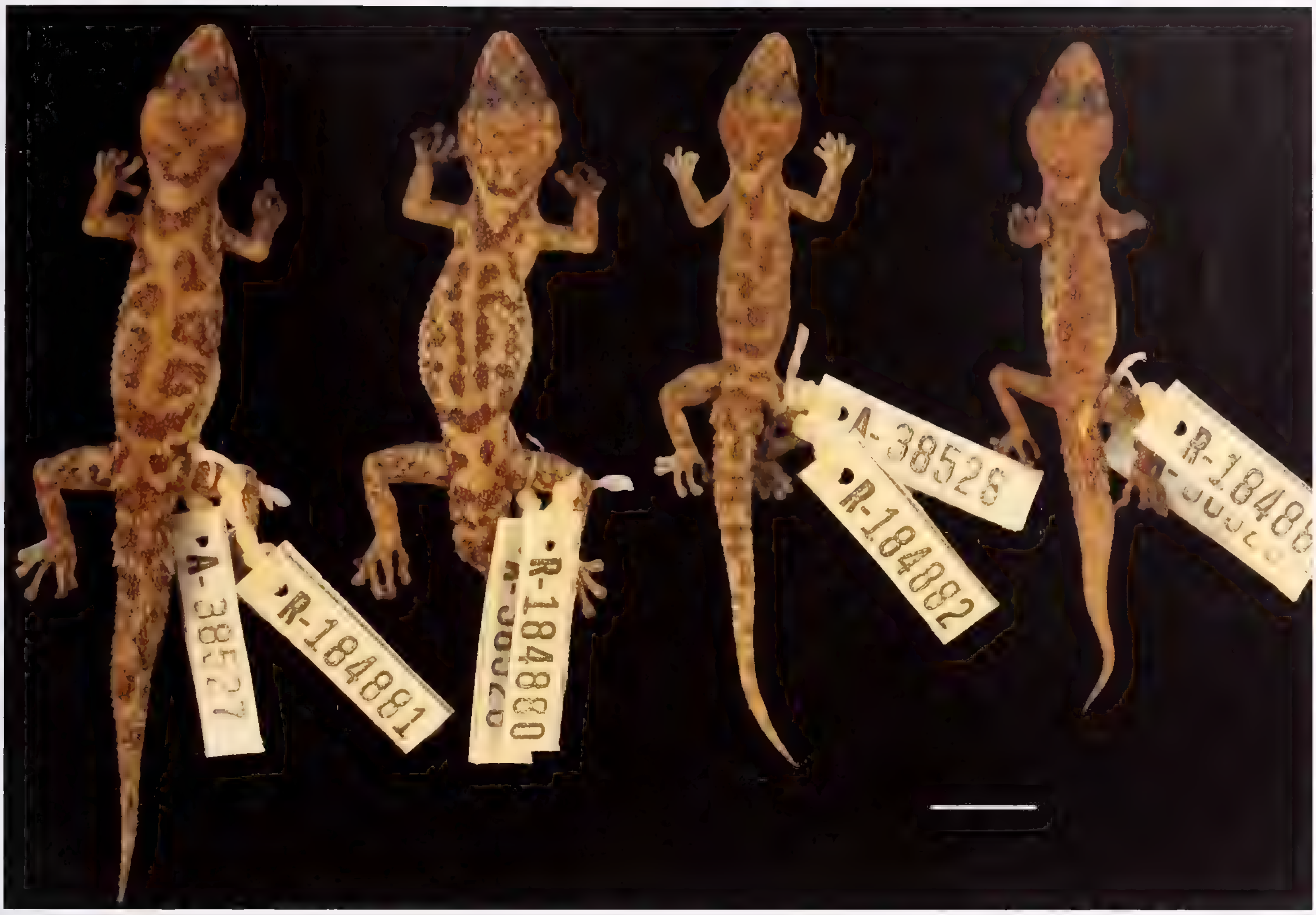

Fig. 5. Paratype series of *Pachydactylus boehmei* sp. n. showing variation in the dorsal color pattern and degree of pattern boldness. Scale bar = 10 mm.

scales of the tail base. In the male paratype, MCZ 184882, the infestation of mites around the tail base and scales of the precloacal spurs was particularly severe.

Phylogenetic affinities. *Pachydactylus boehmei* sp n. is similar in habitus to the other small-bodied, tuberculate members of the "northwestern clade". It is superficially most similar to the neighboring species *P. otaviensis*, although the latter species lacks the rostral-nostril contact that is typical for most members of the clade. Preliminary molecular results suggest that these two species are indeed sister taxa.

Conservation status. *Pachydactytlus boehmei* sp n. does not occur in any protected areas. At its type locality it is undisturbed and the jagged, rocky terrain precludes human encroachment into its specific habitat. However, depending upon the extent of its actual range it may be under some threat from local mining activity in some places. Until such time as the species' distribution and threats can be evaluated more fully, I recommend that it be considered Data Defficient under the IUCN threat category system.

DISCUSSION

The discovery of this apparently range-restricted species highlights Namibia's high biodiversity and endemism (Maggs et al. 1998). M. Griffin (1998) identified 55 reptile species as being strictly or primarily endemic to Namibia, but recent discoveries, particularly in *Pachydactylus* (Bauer et al. 2002, 2006a; Bauer & Lamb 2003) have increased this to approximately 70. The "northwestern clade" of *Pachydactylus* is particularly diverse along the Northern Namibian Escarpment (*sensu* Irish 2002), which corresponds roughly to the Kaokoveld center of Floral Endemism (Volk 1966; van Wyk & Smith 2001) and is recognized as a regional center of endemism for reptiles in general (Crowe 1990; Simmons et al. 1998; Griffin 2000). The Otavi Highlands have also been ranked as an area of high biodiversity importance (Irish 2002), but like the Waterberg to the south, the relatively low relief (a maximum of 2155 m in surrounding plains of 1200–1500 m) and accessibility to surrounding areas that promotes diversity also decreases the prospects for long-term isolation and, consequently, endemism. Thus, it is somewhat surprising that two species of *Pachydactylus*,

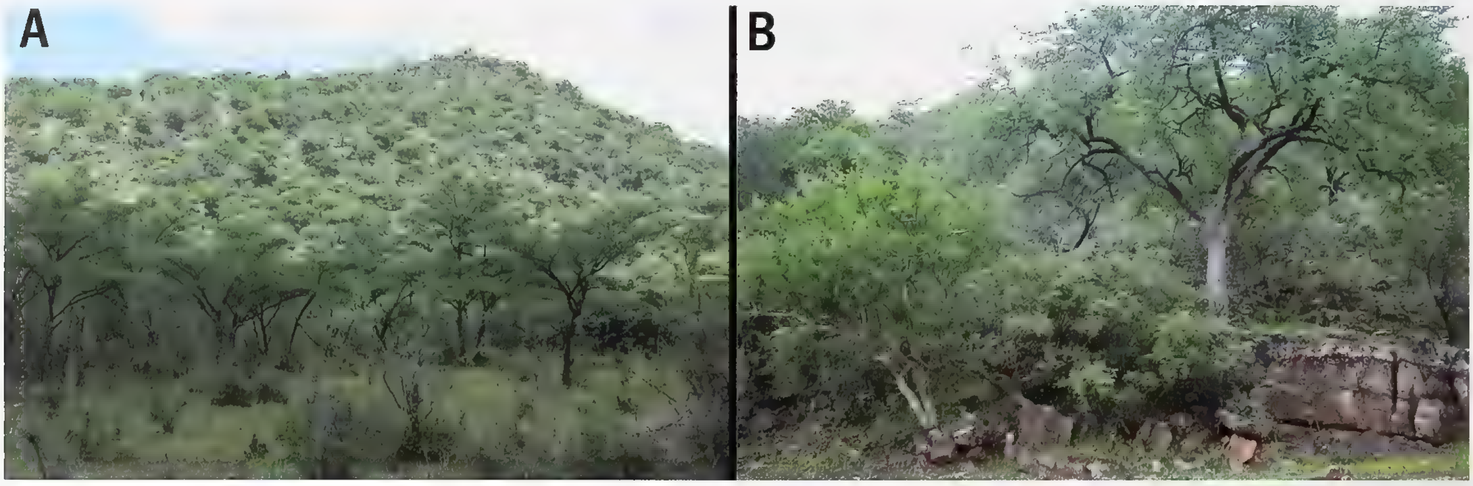

Fig. 6. Habitat of *Pachydactylus boehmei* sp. n. in the Otavi Highlands: (A) View of typical dolomite hill. (B) Broken dolomite providing cracks and fissures as retreat sites for geckos. Photos by Elizabeth Scott.

P. otaviensis and *P. boehmei* sp n., appear to be restricted to this region. Bauer (1999 [2000]) emphasized the role of substrate specificity as a cladogeneic agent in *Pachydactylus* and it seems likely that dependence on microhabitats provided by the dolomite outcrops of the Otaviberge has isolated these species from rest of the "northwestern clade". Other groups of organisms that respond similarly to historical ecological conditions should be expected to show similar patterns of endemism and indeed this is the case in scorpions (R.E. Griffin 1998), which include many substrate specific rupicolous species, such as the bothriurid *Lisposoma josehermana* Lamoral, 1979, which is largely restricted to the Otavi Highlands (Prendini 2003, 2005).

Despite over 50 years of relatively intense study (e.g., Mertens 1955, 1971; Haacke 1965; van den Elzen 1978; Bauer et al. 1993; Griffin, 2000, 2003), novel herpetological taxa continue to be discovered in Namibia on a regular basis. That *Pachydactylus boehmei* sp n. occurs in a densely-populated (by Namibian standards) agricultural district with excellent road access demonstrates that even "well known" parts of the country remain understudied.

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APPENDIX

Comparative specimens examined

See Bauer et al. (2006ab) for a list of *P. weberi* group, *P. otaviensis*, and *P. sansteynae* specimens examined, Bauer & Branch (1995) for a list of *P. punctatus* and *P. scherzi* examined, and Bauer et al. (2002) for a list of *P. angolensis*, *P. scutatus* and *P. parascutatus* examined. Only specimens not included in these publications are listed below. For localities without precise coordinates quarter degree square (QDS) references have been provided when possible. Each single degree square is subdivided into four quarter degrees, designated A–D (A=NW quadrant, B=NE quadrant, C=SW quadrant, D=SE quadrant). Each quarter degree is in turn divided into four similarly designated divisions, yielding a basic unit one sixteenth of a degree square, or one quarter of a degree on a side (e.g., 1915Ac represents the unit bounded by 19°15'S and 19°30'S and 15°00'S and 15°15E). All QDS references in this paper refer to degrees South and East.

P. angolensis: **Angola: Namibe Province:** San Nicolau (1412Ab): TM 25454–55, 25459, 25476, 25478–79; Saco de Giraul: TM 40328–30, TM 46558; Lucira (1312Dc): TM 41172, 24406, 24445, 24449; Lungo: TM 24406; **Benguela Province**: Hanha, 20 km N of Lobito (1213Ab); 24 km S Benguela: TM 39110–11; 30 km N of Dombe Grande: TM 41266.

P. bicolor: **Namibia: Erongo Region: Karibib District:** 47 mi E Hentiesbaai: CAS 126210; 20 km W Karibib: MCZ R163282–83; **Swakopmund District:** 29.0 km N of Swakopmund (22°25'38"S, 14°27'53"E): CAS 214576; 31.1 km N Swakopmund on Hentiesbaai Rd. (22°25'42"S, 14°27'43"E): MCZ R184218–20, 184225; Messum Crater (21°26'25.8"S, 14°13'12.9"E): CAS 214814; **Kunene Region: Khorixas District:** Torrabaai Rd, 63.4 km W of Kamanjab (19°41'00"S, 14°19'10"E): CAS 223912–15; Torrabaai Rd, 58 km W of Kamanjab (19°39'20"S, 14°21'10"E): CAS 223927–28; Torrabaai Rd, 56.7 km W of Franken entrance: CAS 176284–85; Torrabaai Rd, 37.8 km W of Franken entrance: CAS 176292–93; Kamanjab-Torrabaai Rd, Grootberg Pass (19°50.584'S, 14°07.696'E): CAS 193675; Kamanjab-Torrabaai Rd, 59.3 km W of Kamanjab (19°39.100'S, 14°21.335'E): CAS 193680; Torra Bay Rd, 48 km W of Kamanjab, (19°39'14"S, 14°21'03"E): CAS 214661–63; Torra Bay Rd, 68 km W of Kamanjab, (19°43'00"S, 14°18'40"E): CAS 21468–89; Torra Bay Rd, 74.2 km W of Kamanjab (19°45'40"S, 14°17'03"E): CAS 214693–96; E side of Road 3706, 19.3 km N of entrance to Palmwag: CAS 175344; Torrabaai Rd, 108.9 km W of Kamanjab: CAS 176101–08; Torrabaai Rd, 101.7 km W of Kamanjab: CAS 176116–19; Torrabaai Rd, 95.9 km W of Kamanjab: CAS 176126–31; Torrabaai Rd, 44 km W of Kamanjab: CAS 176151; Hentiesbaai-Uis Rd, 24 km W of Hwy C35 (21°18'17"S, 14°35'14"E): CAS 206959; 25 km E of Grootberg Pass: CAS 206960; ~60 km W. Kamanjab on Torra Bay Rd. (19°40'57"S, 14°19'09"E): MCZ R184919; 31.9 km E Grootberg Pass (19°40'57"S, 14°19'09"E): MCZ R184197–98; 62.8 km W Kamanjab Rest Camp on Rd. to Grootberg Pass (19°40'56"S, 14°19'08"E): MCZ R185753–55; 67.5 km W Kamanjab on Torrabaai Rd. (19°43'00"S, 14°18'44"E): MCZ R183766; Hobatere Lodge, 2.5 km from main gate (19°18'07"S, 14°27'26"E): MCZ R184934–35; **Opuwo District:** Kamanjab-Ruacana Rd, 98.4 km N of Kamanjab: CAS 193719; Opuwo-Okangwati Rd, Otjivize (17°37.188 S, 13°27.535 E): CAS 193731; **Outjo District:** 17 mi S of Outjo: CAS 85944; Farm Franken: CAS 175347–53, 175360–74, 176066–68, 176176–77; Farm Franken, Haus Franken: CAS 176261–62; Farm Franken, vic. Haus Franken:

CAS 176278; 62.0 km E Kamanjab, Farm Amolinda (19°48’29”S, 15°22’46”E): MCZ R185745–47; Kamanjab Rest Camp, 3 km W Kamanjab(19°37’48”S, 14°48’57”E): MCZ R184887, 184894–97.

P. caraculicus: **Angola: Namibe Province:** 36 mi. northwest of Mocamedes [Namibe]: CAS 85959; **Namibia: Kunene Region: Opuwo District:** Okangwati-Epupa Rd, 43.4 km N of Okangwati: CAS 193799; 193804–05; 41.9 km N. of Okanguati on Epupa Falls Rd: CAS 206980; 32 km S Epupa Falls on Okangwati Rd. (17°14´09”S, 13°13´45”): MCZ R185767.

P. gaiasensis: **Namibia: Kunene Region: Khorixas District:** vic. Gai-as (20°47’18”S, 14°06’44”): CAS 214626–28; 22.4 km N Ugab River on road to Gai-as (20°46’59”S, 14°06’31”, 520 m a.s.l.): AMB 7568-69 (NMN), MCZ R184169-70, R184248; Gai-As (20°46’45”S, 14°04’30”E, 520 m): AMB 8484 (NMN), MCZ Z-37873 (NMN), MCZ R184181, R184192–93; Gai-As (20°46´46´´S,14°04´29´´E): MCZ R185967–75, 185979–80; “False Gai-As” (20°47’14.9”S, 14°06’44.6”E): MCZ Z-37853–54 (NMN), MCZ R184185, R184187; 7 km E Gai-as (20°47’S, 14°07’E): TM 68962–66; Messem Crater, 21 26.430 S, 14 13.215 E : CAS 214800; Messum Mts. (2114Ac): TM 56346; Farm Twyfelfontein: TM 42182; near Gai-as, ~20 mi N Brandberg: TM 32868–80 [paratypes].

P. oreophilus: **Angola: Namibe Province:** Caraculo (15°01’S, 12°40’E): TM 24519–25, 24452; 20 km W Virei: TM 41011–15; Tambor: TM 40532–34; 6 km S Rio Coroca towards Iona: TM 40575–76; Mutiambo River on road to Lucira: TM 41088; Furnas: TM 40561–62; Namibe 7 km from Iona towards Oncocau, Iona Reserve: TM 40762; Assuñcao: TM 40152; Saiona River, 25 km NW Cainde: TM 40976–77; **Benguela Province:** 35 km S Dombe Grande towards Lucira: TM 41246; **Namibia: Kunene Region: Opuwo District:** near Purros (18°46’S, 12°59E); TM 68465–67; Hoanib River (19°18’S, 13°15’E): TM 64185; Hoanib River, 44 km E Mudorib River (19°18’S, 13°15’E): TM 56889; Epupa Falls (16°59’S, 13°17’E): TM 38771–72, 71579; 6 km S Ohnborimbonga (1712Bb): TM 49084–85; Marienfluß, 40 mls S Kunene: TM 32532; near Otjinende, Kaokoveld (1712Db): TM 49219; Epupa (1613Cc): TM 47775; N Okangwati on Epupa Falls Rd. (17°17´24´´S, 13°09´31´´E): MCZ R185769; Paracamp, Sesfontein (19°07´52´´S, 13°35´17´´E): MCZ R-184945–47; Paracamp, Sesfontein (19°07´55”S, 13°35´20”E): MCZ R184290; ca 2 km N of Sesfontein, Para Camp (19°07’28”S, 13°35’29”E): CAS 214736, 214754; ca 4 km N of Sesfontein, Para Campsite (19°07’56”S, 13° 35’18”E): CAS 223919–22.

P. otaviensis: **Namibia: Oshikoto Region: Tsumeb District:** Farm Varianto (19°22´46”S, 17°44´27”E): MCZ R184867.

P. parascutatus: **Namibia: Kunene Region: Opuwo District:** Mudorib River, 12 km from Hoanib River (19°23’S, 13°17’E): TM 68488–92; Okamungodona, 15 km W Orawanji (18°49’S, 13°39’E): TM 71519–21; Otunungwa, Kaokoveld: TM 32401–03; Kharu-gaiseb River (19°45’S, 13°25’E): TM 68517–18; Bottom of Van Zyl’s Pass (1712Da): TM 71497; 37 km N Sesfontein towards Kaoko Otavi (1813Dc): TM 48876–77; Otjiu, Kaokoveld: TM 32358; 32858–59; 18 miles SW Orupembe: TM 31494; Otjinungwa, Kaokoveld: TM 32860; 4 km NW Etenga towards Omborombongo (1712Bd): TM 49060; Nangolo Flats (1712Ad): TM 24322; Otjiunongua (1712Ab): TM 32546; Sesfontein (19°07’S, 13°37’E): TM 79078; Ongongo/Kaoko: ZFMK 66434.

P. scutatus: Angola: Namibe Province: Iona, Iona Reserve: TM 40751; Espinheira, Iona Reserve: TM 40615–18; 6 km S Rio Coroca, Iona: TM 40577; Namibia: Erongo Region: Omaruru District: Ugab River Bridge near Brandberg W. Mine: TM 36463; Ugab River (20°58’S, 14°12’E): TM 49708; Tsisab Gorge, Brandberg (2114Ba): TM 79286; Brandberg: SMF 58564; Sraussenhöhle an der Jochmannswald, Brandberg: SMF 45658; Kunene Region: Khorixas District: Farm Palmwag (19°53’S, 13°53’E): TM 56865; Farm Paderborn (1914Dd): TM 17302; Kamanjab (1914Db): TM 17209, 17270, 36372; Damaraland (20°30’S, 13°49’E): TM 68754; Farm Huab (1914Db): TM 17338; Farm Palmfontein (part of Grootberg): TM 36465; Farm Blauwpoort (2014cb): TM 49419; Agab Spring (20°05’S, 13°50’E): TM 56936; Opuwo District: Epupa Falls (16°59’S, 13°17’E): TM 71352–53; Otjiu, Kaokoveld: TM 32539.

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A new *Tarentola* subspecies (Reptilia: Gekkonidae) endemic to Tunisia

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Abstract. Mitochondrial DNA sequences as well as morphological characters reveal that geckos of the genus *Tarentola* from Libya and central Tunisia are a monophyletic group which is different from both *T. mauritanica* and *T. deserti*. Consequently, we elevate the former subspecies *T. mauritanica fascicularis* to species rank. Together with *T. neglecta* and *T. mindiae*, *T. fascicularis* constitutes the sister group of *T. deserti*. *Tarentola fascicularis* comprises several evolutionary units, one of which we describe here as a subspecies endemic to south-central Tunisia.

Key words. *Tarentola*, gecko, Tunisia, Libya, North Africa, taxonomy.

INTRODUCTION

The Mediterranean geckos of the genus *Tarentola* Gray, 1825 are classified in the nominative subgenus *Tarentola*. The Canary Islands are inhabited by geckos of the subgenera *Tarentola* (Eastern Canaries) and *Makariogecko* (western Canaries, Selvagens and Cape Verde Islands) whereas other subgenera inhabit sub-Saharan Africa and the Caribbean (Joger 1984a, b). To date, the nominative subgenus comprises the following species: *Tarentola mauritanica* (L., 1758), *T. deserti* Boulenger, 1891, *T. angustimentalis* Steindachner, 1891, *T. boehmei* Joger, 1984. Although no subspecies have been described in the latter three species, the North African populations of *T. mauritanica* have been assigned to a number of subspecies; including, *T. m. mauritanica*, *T. m. fascicularis* (Daudin, 1802) from Egypt, *T. m. juliae* Joger, 1984, and *T. m. pallida* Geniez et al., 1999, both from Morocco. *Tarentola angustimentalis* (eastern Canary Islands) and *T. deserti* (northern margin of the Sahara Desert) used to be classified as subspecies of *T. mauritanica* until they were elevated to species rank (Joger 1984b). In the case of *T. deserti*, sympatric records of *T. deserti* and *T. mauritanica* in Tunisia and Algeria gave reason to assume that these were separate biological species.

Tarentola deserti and *T. mauritanica* can be distinguished from each other in a number of characters (Table 1, Figs 1 and 2). In the field, *T. deserti* is characterized often by its very large size, pale, often rosy body colour and a yellowish or ochre brown coloured iris, whereas typical *T. mauritanica* is smaller and has a grey body and iris colouration.

In contrast, in south-central Tunisia (Bou Hedma National Park and areas to the north of the Chott al Djerid salt pan) populations of *Tarentola* were found that show a mixture of characters of both species (Table 1, Fig. 3). Their size is smaller than *T. deserti*, but body and eye colour are close to *T. deserti* (Joger & Bischoff 1989; Joger 2003). A preliminary study of morphological and electrophoretic characters (Willand 1997; Joger et al. 1998) showed that these geckos cluster morphologically with *T. mauritanica* (yet not with any of its described subspecies), whereas their dorsal colour and pattern is close to *T. deserti* and their blood plasma protein alleles are distinct and not shared by neither *T. mauritanica* nor *T. deserti*.

Previous molecular genetic studies (Carranza et al. 2002; Rato et al. 2010) of North African *Tarentola* were biased in that they concentrated on Moroccan populations but largely neglected Tunisian and Libyan populations. In this study, we use both morphological and molecular samples of Tunisian and Libyan *Tarentola* to determine the affinities and clarify the taxonomy of the enigmatic *Tarentola* of south-central Tunisia.

MATERIALS AND METHODS

Animals were collected during several trips to Morocco, Algeria, Tunisia (U.J.) and Libya (I.B.). Specimens from Egypt were kindly provided by Sherif Baha El Din and Adel Ibrahim. Blood samples were taken by heart puncture or from muscle tissue of dead animals and preserved

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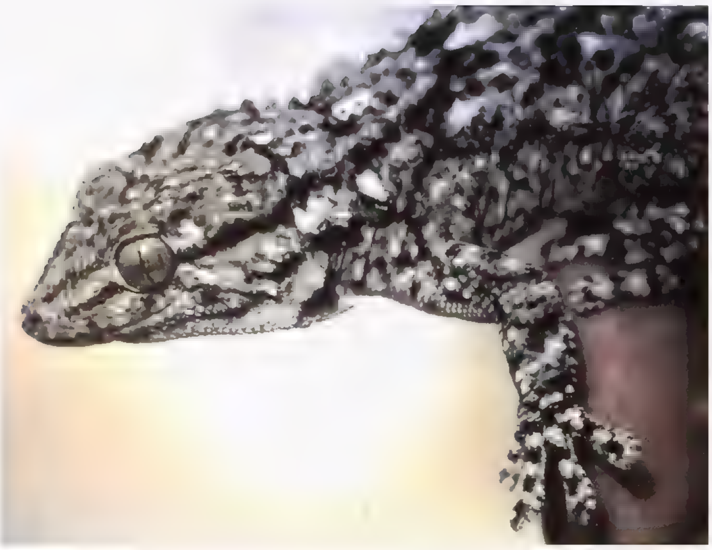

Fig. 1. *Tarentola mauritanica* (Tunisia).

Table 1. Distinguishing characters of North African *Tarentola* (mean ± standard deviation). Significant differences from *T.* sp. (Tunisia) are highlighted (in bold). Significance values are given for males (first value) and females separately (if different). *** P<0.001; ** P<0.01; * P<0.05; n.s. not significant.

characters	*T.mauritanica* - Tunisia N=22	*T.*sp.- Tunisia N=15	*T.*sp.-complex-Libya N=139	*T.deserti* ssp.- Libya N=73	*T.d.deserti* - N-Africa N=24
Maximal head + body length	83.5	86	79	77.7	103.3
Lamellae under 1st toe	11.0 ± 1.0	**10.3 ± 0.8**	**10.9 ± 0.6 n.s./*****	**11.0 ± 0.7 n.s./*****	**12.7 ± 1.1** ***
Lamellae under 4th toe	**16.8 ± 1.0** ***	**15.3 ± 1.0**	15.8 ± 1.0	**15.9 ± 0.8 n.s./****	**18.2 ± 1.3** ***
Lamellae under 5th toe	20.5 ± 1.5	**19.7 ± 1.1**	20.2 ± 1.6	20.3 ± 1.1	**22.8 ± 1.3** ***
Ventral scales	37.7 ± 3.3	**34.3 ± 2.7**	36.6 ± 3.2	**40.0 ± 2.7** ***	**40.1 ± 2.0** ***
Dorsal tubercles	13.5 ± 1.0	**12.1 ± 0.5**	12.8 ±1.4	**13.4 ± 0.9** **/***	12.2 ± 0.7
Gular scales	41.1 ± 4.7	**43.3 ± 6.6**	43.3 ± 4.7	45.3 ± 5.4	**56.0 ± 6.9** ***
Interorbitals	**14.9 ± 1.2** **	**13.7 ± 1.0**	**14.9 ± 0.7** ***	**14.6 ± 0.9** **	14.5 ±0.7
Infralabials	8.0 ± 0.7	**7.9 ± 0.7**	7.9 ± 0.5	8.0 ± 0.5	**8.8 ± 0.6** ***
Supralabials	7.8 ± 0.6	7.7 ± 0.7	7.9 ± 0.5	8.0 ± 0.4	8.0 ± 0.4
Relative inter-orbital width	0.38 ± 0.03 0.39 ± 0.02	**0.42 ± 0.04** **0.41 ± 0.03**	**0.36 ± 0.04** *** 0.37 ± 0.04 n.s.	**0.36 ± 0.04** *** **0.37 ± 0.05** *	0.43 ± 0.06 0.42 ± 0.04
Relative ear to mental distance	0.84 ± 0.03 0.88 ± 0.06	**0.91 ± 0.03** **0.90 ± 0.03**	**0.66 ± 0.07** *** **0.69 ± 0.21** **	**0.66 ± 0.06** *** **0.68 ± 0.09** ***	0.89 ± 0.04 0.88 ± 0.03

in 96% ethanol. Voucher specimens were preserved in 80% ethanol.

Morphological data were taken as described by Joger (1984a). Measurements were taken to the nearest 0.1 mm and normalized as proportion to body length. Pholidotic counts were taken unaltered.

Operational taxonomic units (OTUs) were defined using a combination of mitochondrial DNA clades and geographic proximity. Linear Discriminant Function Analyses (LDFA) were used to find variables that separate the groups. Principal Component Analyses (PCA) were applied to see whether groups are distinguishable without previous definition of OTUs. Significance of character differences were tested with t-tests.

DNA was extracted from the preserved samples using standard procedures. Universal primers were used to amplify mitochondrial 12S rRNA (372 bp) and 16s rRNA (2 fragments of 448 and 604 bp). Sequences were determined using an automated sequencer, and aligned with CLUSTAL-W omitting gaps. Sequences from Genbank were added in some cases. A sequence of a paratype of the new subspecies was submitted to GenBank (IB47: HQ437282). Phylogenetic trees were constructed using a Bayesian Markov Chain Monte Carlo inference applying an evolution model suggested by MODELTEST 3.7. Statistical support for branches was indicated by posterior probability values (MrBayes).

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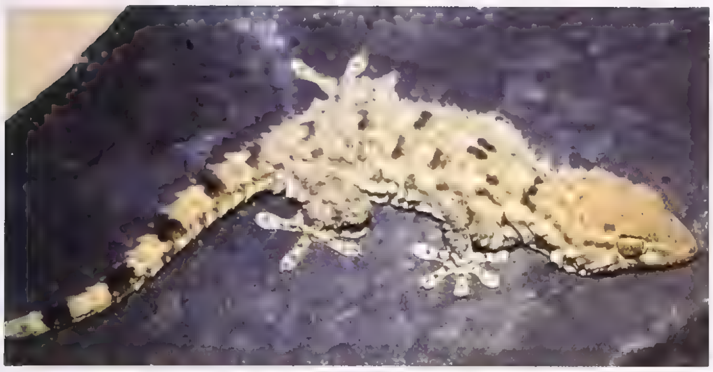

Fig. 2. *Tarentola deserti* (Biskra, Algeria).

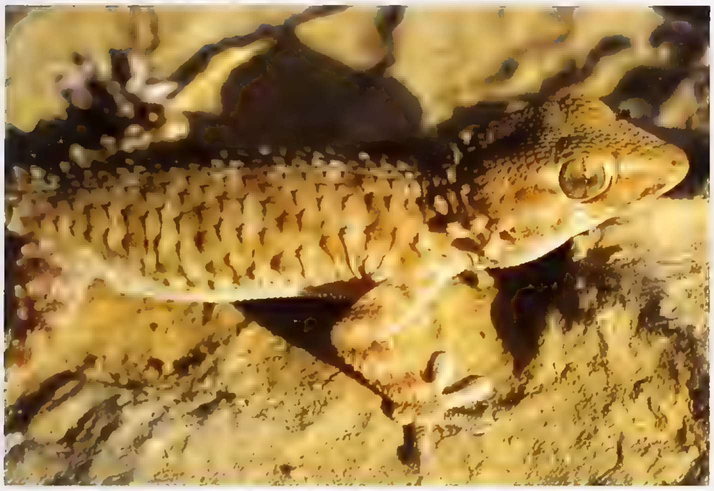

Fig. 3. *Tarentola* sp. (Bou Hedma, Tunisia).

RESULTS

Morphological comparisons

CDF plots (Figs 4a, b) show that *T.* sp. (Tunisia) are different morphologically from *T. deserti* as well as from undescribed *Tarentola* from western Libya ('*T.* sp. complex'). When North African populations of *T. mauritanica* are compared with *T.* sp. (Tunisia), only males appear distinct, whereas females cluster with *T. mauritanica* from Tunisia and Morocco (Fig. 5b).

Significantly different characters which distinguish Tunisian *Tarentola* from Libyan and other North African populations are shown in Table 1.

Molecular genetic affinities

Mitochondrial gene sequences (12S rRNA, 16s rRNA) reveal that *T.* sp. (Tunisia) does not cluster with *T. mauritanica* but with undescribed Libyan *Tarentola* (Fig. 8). These Libyan populations form several geographically restricted, monophyletic clades; the most western ones are sister to *T.* sp. (Tunisia) – yet with rather low statistical support. *Tarentola deserti*, *T. mauritanica fascicularis* (Egypt, East Libya), and even *T. neglecta* appear more closely related to the western Libyan-Tunisian group of clades than *T. m. mauritanica*. This is highly supported statistically (1.00 posterior probability). It is noteworthy that the populations near the (neo-) type locality of *T. m.*

Table 2. Uncorrected "P" distance between main clades, estimated of evolutionary divergence between sequences, based on pairwise analysis of 1433 bp mtDNA sequences.

	Clade A	Clade B	Clade C	Clade D	Clade E	Clade F	Clade G	Clade H
Clade A								
Clade B	0.0921							
Clade C	0.0972	0.0704						
Clade D	0.1180	0.0977	0.0692					
Clade E	0.1052	0.0853	0.0562	0.0705				
Clade F	0.0974	0.0634	0.0630	0.0802	0.0645			
Clade G	0.1145	0.0873	0.0662	0.0665	0.0694	0.0510		
Clade H	0.1141	0.0886	0.0691	0.0711	0.0706	0.0578	0.0270	
Outgroup	0.1234	0.1407	0.1357	0.1545	0.1564	0.1422	0.1531	0.1490

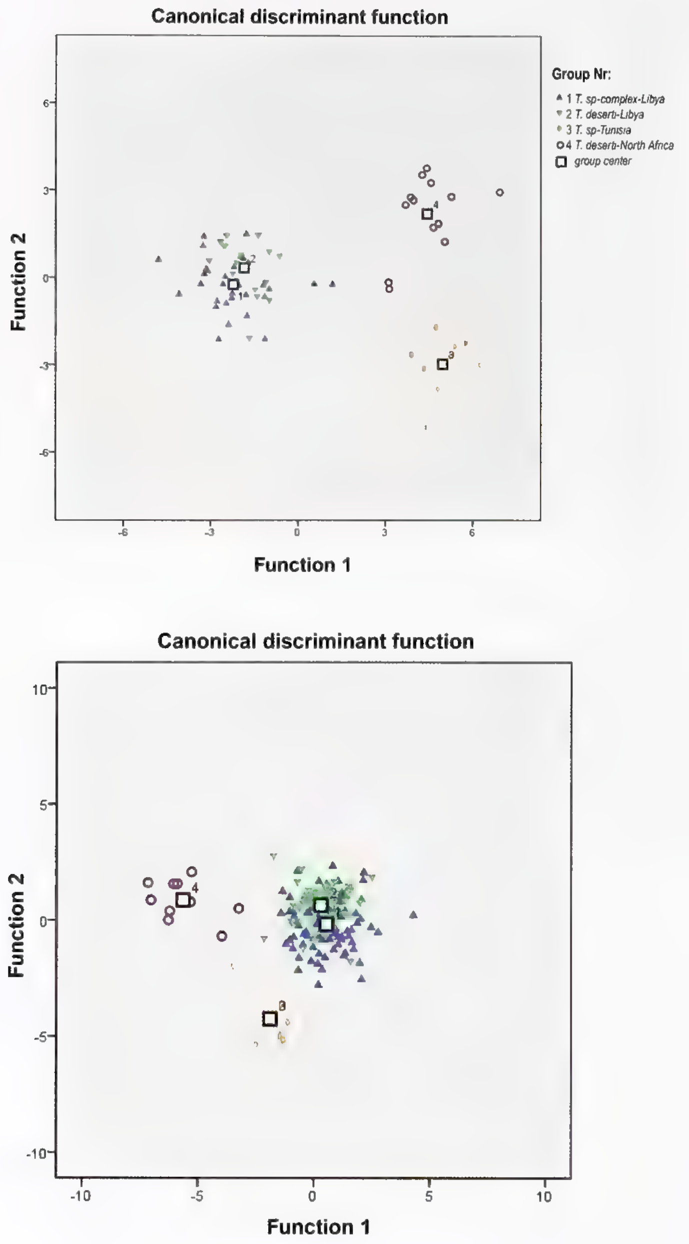

Fig. 4. CDF plots for *Tarentola* sp-Tunisia, *Tarentola deserti*-North Africa, *Tarentola sp*-complex-Libya (western Libyan *T. fascicularis*), and *Tarentola deserti*-Libya; males (above) and females (below).

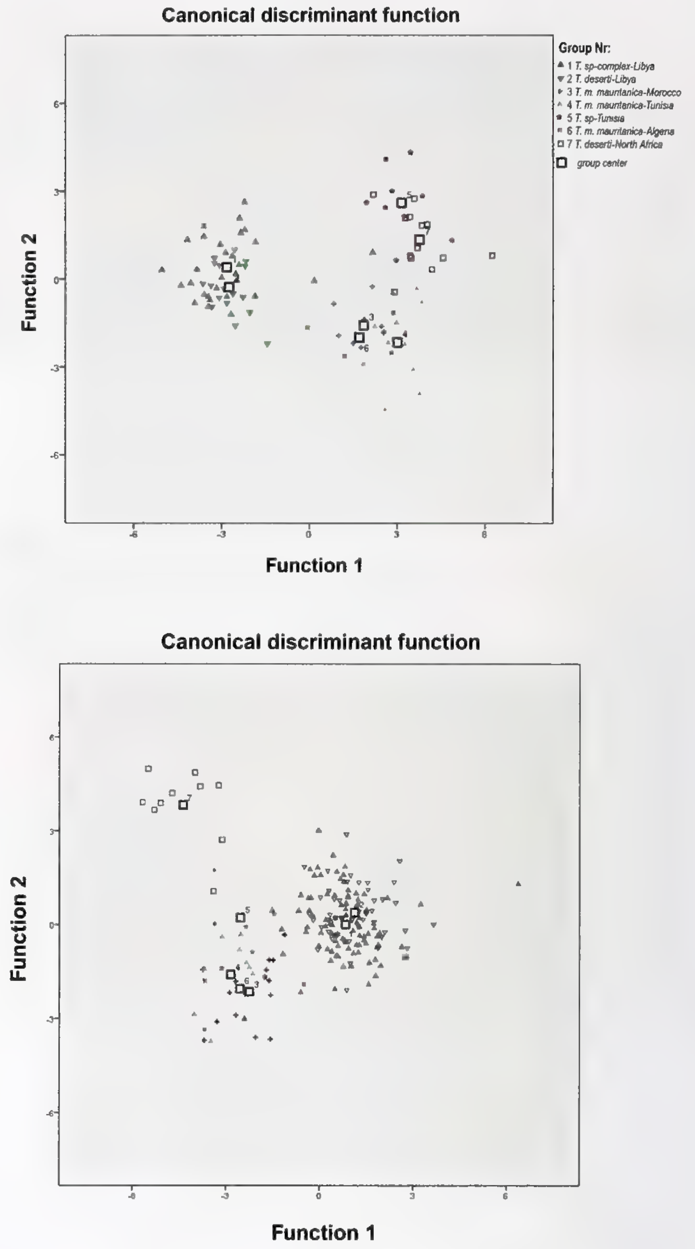

Fig. 5. CDF plots of different populations of North African *Tarentola*, males (above) and females (below) plotted separately.

fascicularis, in East Libyan Cyrenaica, belong to a separate clade (clade D).

Genetic distances among Libyan and Tunisian *Tarentola* clades are provided in Table 2.

Two of the mitochondrial clades occur sympatrically or parapatrically: *T. deserti* (Libya) and '*T.* sp. complex' (clade H) at Itwellia (western Libya), clades C and D along the desert road Tobruk-Ajdabiya in Cyrenaica.

DISCUSSION

Parapatric or sympatric occurrence of mitochondrial clades could be interpreted in different ways: either different biological species or co-existence of two mitochondrial distinct populations in a mixed interbreeding organismal population. In the case of *T. deserti* in NW Libya, there is evidence of the former explanation, as the molecular differences coincide with morphological differences.

Table 3. Variation of the Paratypes (part).

Variable	Mean	Minimum	Maximum	Standard deviation
Lamellae under 1st toe	10.27	9.00	12.00	0.80
Lamellae under 4th toe	15.27	14.00	17.00	0.96
Lamellae under 5th toe	19.67	18.00	21.00	1.11
Ventral scales	34.33	28.00	38.00	2.72
Supraorbital scales	5.73	5.00	6.00	0.46
Dorsal tubercles	12.13	12.00	14.00	0.52
Gular scales	44.21	32.00	55.00	5.82
Interorbital scales	13.73	12.00	15.00	0.96
Head length	17.18	13.89	21.03	2.16
Head+body length	56.08	44.12	72.33	7.62
Infralabialia	7.93	7.00	9.00	0.70
Supralabialia	7.73	6.00	9.00	0.70
Relative hindleg length	0.49	0.45	0.51	0.02
Relative head width	0.70	0.62	0.82	0.05
Relative head length	0.31	0.29	0.32	0.01
Relative foreleg length	0.36	0.32	0.40	0.02
Relative ear-snout length	0.90	0.84	0.95	0.03

When a conservative two-species concept (*T. mauritanica* – *T. deserti*) is applied, the mitochondrial tree unambiguously affiliates all sequenced Libyan OTUs with *T. deserti*, and not with *T. mauritanica*. The mitochondrial genetic distance between the central Tunisian *Tarentola*, the Libyan clades and *T. deserti* are lower than between the Tunisian clade and *T. m. mauritanica*. This supports the view that despite some morphological similarity, the Tunisian and Libyan-Egyptian clades are not subspecies of *T. mauritanica*.

Assigning these OTUs to *T. deserti* would, however, create a paraphyletic *T. deserti*, with *T. neglecta* and *T. mindiae* – which are without doubt separate species – within *T. deserti*. The most parsimonious taxonomic solution with regard to the cladogram is to subsume clades C, D, E, G, and H under one separate species.

Morphological data indicate that several of the mitochondrially defined populations, in particular if they occur in desert areas (Sabha in South Libya, Algerian and Tunisian but not Libyan *deserti*, and also a subclade of clade D) can be distinguished by larger size and higher scale counts. These size-linked characters may be locally favoured by environmentally triggered selection. On the other hand, morphological differences do not preclude genetic closeness, and genetically distant clades may share morphological similarity.

In conclusion, the genetically studied *Tarentola* from Libya and Egypt, as well as those from south central Tunisian, should be assigned to *T. fascicularis* (a former subspecies of *T. mauritanica*). Elevation of *fascicularis* to species rank is largely consistent with data of Rato et al. (2010), who distinguished two basal divisions in the subgenus *Tarentola*. One of these branches lead to *T. deserti* and *T. boehmei*, another to *T. angustimentalis* and *T. mauritanica* from Europe, Morocco, Algeria and northern Tunisia on one side, and to *T. (m.) fascicularis* and *Tarentola* from Lampedusa and Conigli Islands on the other side. Single individuals of '*T. mauritanica*' from Algeria and of '*T. deserti*' from Morocco were loosely connected to the latter clade, but we do not know which taxa were really represented by those samples. The Tunisian samples used by these authors clustered with *T. m. mauritanica*, but they were exclusively from northwestern Tunisia. True *T. mauritanica* exist in coastal areas of Tunisia and western Libya.

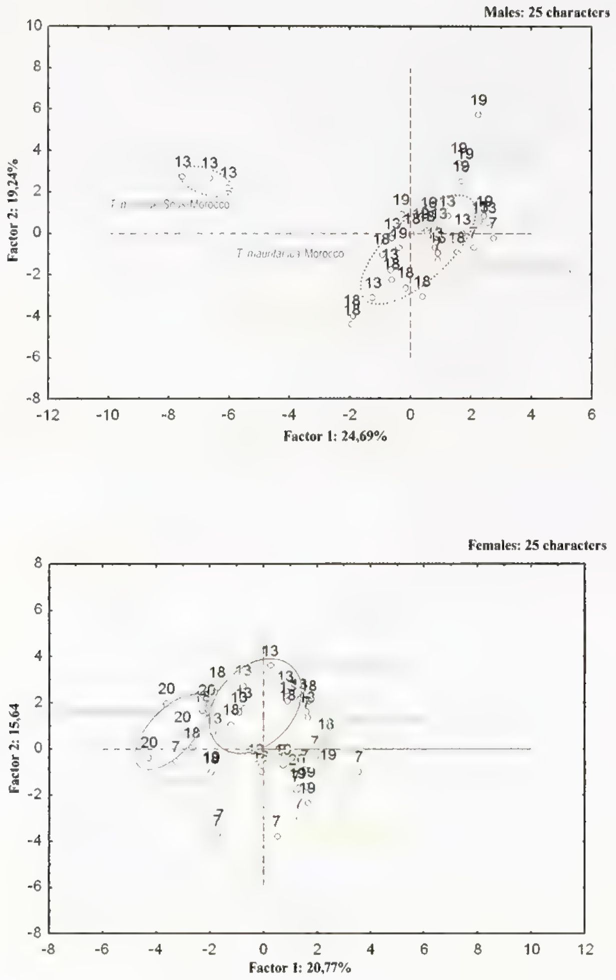

Fig. 6. PCA of *Tarentola* sp. (Tunisia), *T. m. fascicularis* (Libya), and different populations of *T. mauritanica*. Males above, females below.

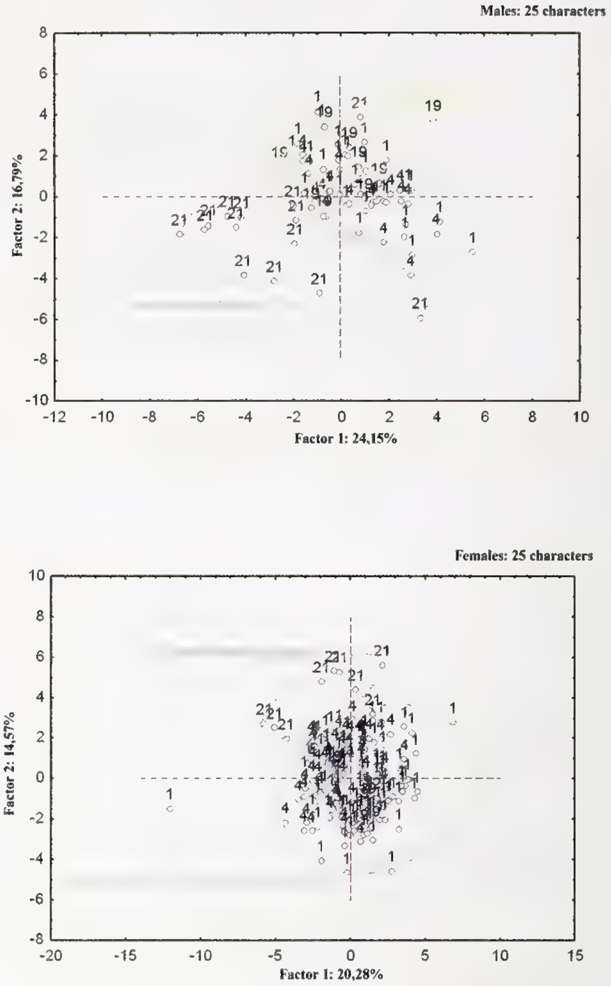

Fig. 7. PCA of *Tarentola deserti* (Libyan populations), *T.* sp. (western population of *T. fascicularis*, Libya) and *T.* sp. (Tunisia). Males above, females below.

In Tunisia, *T. deserti* exists in the extreme south (south-southeast of the Chott al Djerid) and a new subspecies of *T. fascicularis* in south central Tunisia between the Chott al Djerid and Djebel Bou Hedma. The description of this new subspecies is presented below.

Description of a new subspecies of *Tarentola fascicularis*

Tarentola fascicularis n. comb.

Gecko fascicularis Daudin, 1802

Tarentola mauritanica mauritanica, Loveridge 1947 (partim, non Linnaeus 1768)

Tarentola mauritanica fascicularis, Joger 1984

Terra typica (after designation of a neotype by Joger [1984]): Ain Teyanah, 20 km south of Benghazi, Libya.

Tarentola fascicularis wolfgangi ssp. n.

Holotype. State Natural History Museum Braunschweig (SNHM-BS) N 41980, male, collected 19 August 1998 by Ulrich Joger (Fig. 9).

Terra typica. Bou Hedma National Park, Tunisia (34.24'N, 9.23'E).

Paratypes. 33 specimens; SNHM-BS 39920-39930, 41981, Bou Hedma; HLMD 2105-2109, 2265-2271, 2363-2366, Bou Hedma; HLMD 1238-1240, Djebel Orbata/El Guettar; ZFMK 49525, 49526, Djebel Orbata: El Guettar.

Description of holotype. Measurements (mm). Head + body 61.0, tail 71.4, head length 19.8, head width 14.7, head height 10.8, interorbital width 8.4, distance snout-ear 17.7; foreleg 23.9, hindleg 30.2, distance between foreleg and hindleg 25.1, 4th toe length 5.1, toe width 2.0, diameter of eye 4.5.

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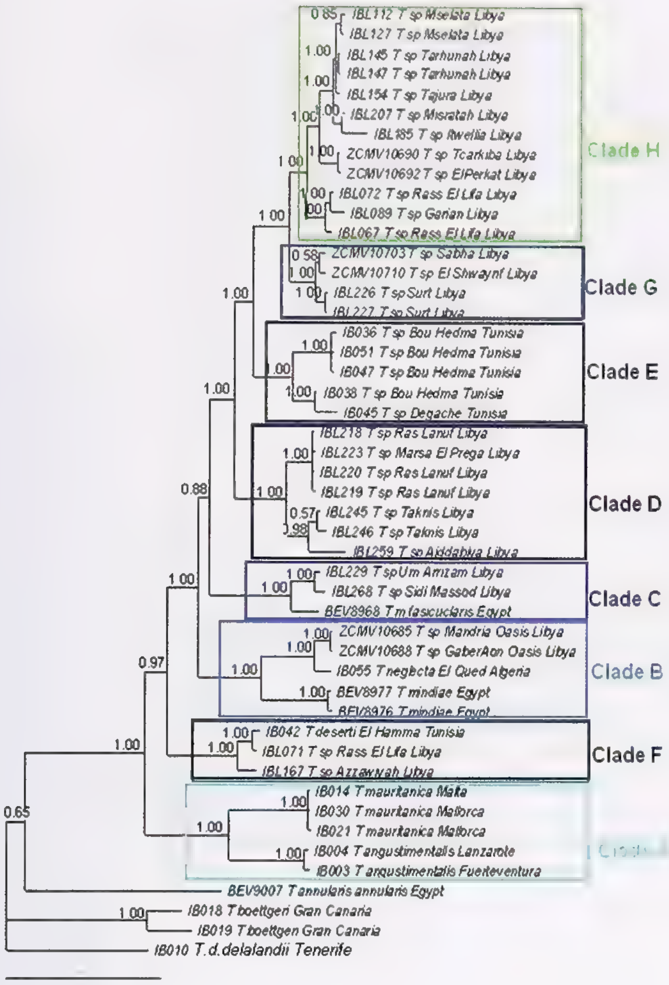
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IBL127 T sp Mselata Libya
IBL145 T sp Tarhunah Libya
IBL147 T sp Tarhunah Libya
IBL154 T sp Tajura Libya
IBL207 T sp Misratah Libya
IBL185 T sp Itwellia Libya
ZCMV10690 T sp Tcarkiba Libya
ZCMV10692 T sp ElPerkat Libya
IBL072 T sp Rass El Lifa Libya
IBL089 T sp Garian Libya
IBL067 T sp Rass El Lifa Libya
Clade H
ZCMV10703 T sp Sabha Libya
ZCMV10710 T sp El Shwaynf Libya
IBL226 T sp Surt Libya
IBL227 T sp Surt Libya
Clade G
IB036 T sp Bou Hedma Tunisia
IB051 T sp Bou Hedma Tunisia
IB047 T sp Bou Hedma Tunisia
IB038 T sp Bou Hedma Tunisia
IB045 T sp Degache Tunisia
Clade E
IBL218 T sp Ras Lanuf Libya
IBL223 T sp Marsa El Prega Libya
IBL220 T sp Ras Lanuf Libya
IBL219 T sp Ras Lanuf Libya
IBL245 T sp Taknis Libya
IBL246 T sp Taknis Libya
IBL259 T sp Aiddabiya Libya
Clade D
IBL229 T sp Um Arrizam Libya
IBL268 T sp Sidi Massod Libya
BEV8968 T m fasicuclaris Egypt
Clade C
ZCMV10685 T sp Mandria Oasis Libya
ZCMV10688 T sp GaberAon Oasis Libya
IB055 T neglecta El Qued Algeria
BEV8977 T mindiae Egypt
BEV8976 T mindiae Egypt
Clade B
IB042 T deserti El Hamma Tunisia
IBL071 T sp Rass El Lifa Libya
IBL167 T sp Azzawyah Libya
Clade F
IB014 T mauritanica Malta
IB030 T mauritanica Mallorca
IB021 T mauritanica Mallorca
IB004 T angustimentalis Lanzarote
IB003 T angustimentalis Fuerteventura
BEV9007 T annularis annularis Egypt
IB018 T boettgeri Gran Canaria
IB019 T boettgeri Gran Canaria
IB010 T.d.delalandii Tenerife
0.85
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Fig. 8. 50% majority-rule consensus tree obtained from Bayesian MCMC analysis, based on 1433 bp mtDNA sequences, depicting the relationships among haplotypes. *Tarentola delalandii* designated as outgroup and Bayesian posterior probability values are given near branches.

Pholidosis. 36 longitudinal rows of ventral scales; 12 longitudinal rows of dorsal tubercles, bearing strong central keel from which barely visible keels derive laterally; 13 lamellae under 1st toe, 15 lamellae under 4th toe, 20 lamellae under 5th toe; 15 interorbital scales, 6 supraorbital scales; gular scales separated from mental by 3 scales, gular scale count 43; 10 supralabials, 7/8 infralabials; rostral divided, touching nostril; nasal scales separated by one scale proximally and one scale distally. Colour (in ethanol) whitish, without any visible pattern.

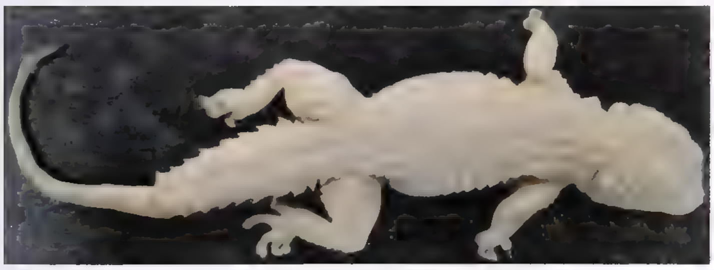

Fig. 9. Holotype of *Tarentola fascicularis wolfgangi* ssp. n.

Variability of paratypes. Colour (in ethanol) light or medium grey dorsally, whitish ventrally. Most specimens bear following pattern: dark line on side of head from eye to above ear. Paired dark spots, followed posteriorly by unpaired whitish spot (without clear margins) distributed on mid-dorsum as follows: one in front of shoulder, one behind shoulder, two on back, one on pelvic region, one on base of tail, followed by 9–10 unpaired half-rings around dorsal part of tail. Scale count variation is shown in Table 3.

Diagnosis. A small subspecies of *T. fascicularis*; maximum recorded body+head length in males 72.3 mm, in females 57.5 mm (up to more than 100 mm in male *T. deserti*, 81 mm in female *T. deserti*; in eastern Libyan *T. fascicularis*, 97 mm can be attained in males of the Ras Lanuf population, yet only 79 mm in *T. fascicularis* ssp. from northwestern Libya).

Tail length usually clearly longer than body+head (index body+head/tail 0.77-1.00; mean 0.84, as opposed to 0.98 in *T. deserti*, 0.96 in *T. f. fascicularis*, and 0.96 in *T. m. mauritanica*). Snout (ear openings to mental) significantly longer than in T. *fascicularis* and *T. deserti* subspecies from Eastern Libya (about 90% of head length as opposed to 60–70%).

Dorsal tubercles in 11–14 (most often 12) longitudinal rows, most often simply keeled (multiply keeled in *T. f. fascicularis*). 19–46 gular scales (45–59 gular scales in *T. d. deserti*). Different from all other Tunisian or Libyan *Tarentola* (except *T. neglecta* group) by lower number of ventral scales (34.3 +/- 2.7) and lower number of lamellae underneath 1st and 4th toes (1st 10.3 +/- 0.8, 4th 15.3 +/- 1.0). 15–22 scale rows or lamellae underneath 5th toes (16-21 in *T. f. fascicularis*, 21–25 in *T. deserti*). Different from Tunisian *T. mauritanica* by lower number of interorbital scales (13.7 +/- 1.0 versus 14.9 +/- 1.2); from Libyan *T. mauritanica* by lower number of sublabials (7.9 +/- 0.7 versus 8.7 +/- 0.7); from western Libyan subspecies of *T. fascicularis* by lower number of interorbital scales (13.7 +/- 1.0 versus 14.9 +/- 0.7). Rostral usually separated from nostril by small scales (in *T. f. fascicularis* rostral usually in contact with nostril).

Dorsal colour in life similar to *T. deserti*: rosy or yellowish, with yellowish iris (grey in *T. m. mauritanica*). Five dark transverse bands across back, often reduced to paired spots.

Distribution. Endemic to Central Tunisia; known from Gafsa (Djebel Orbata) in the West to Bou Hedma in the East, south to Degache and Tozeur at northern banks of Chott al Djérid.

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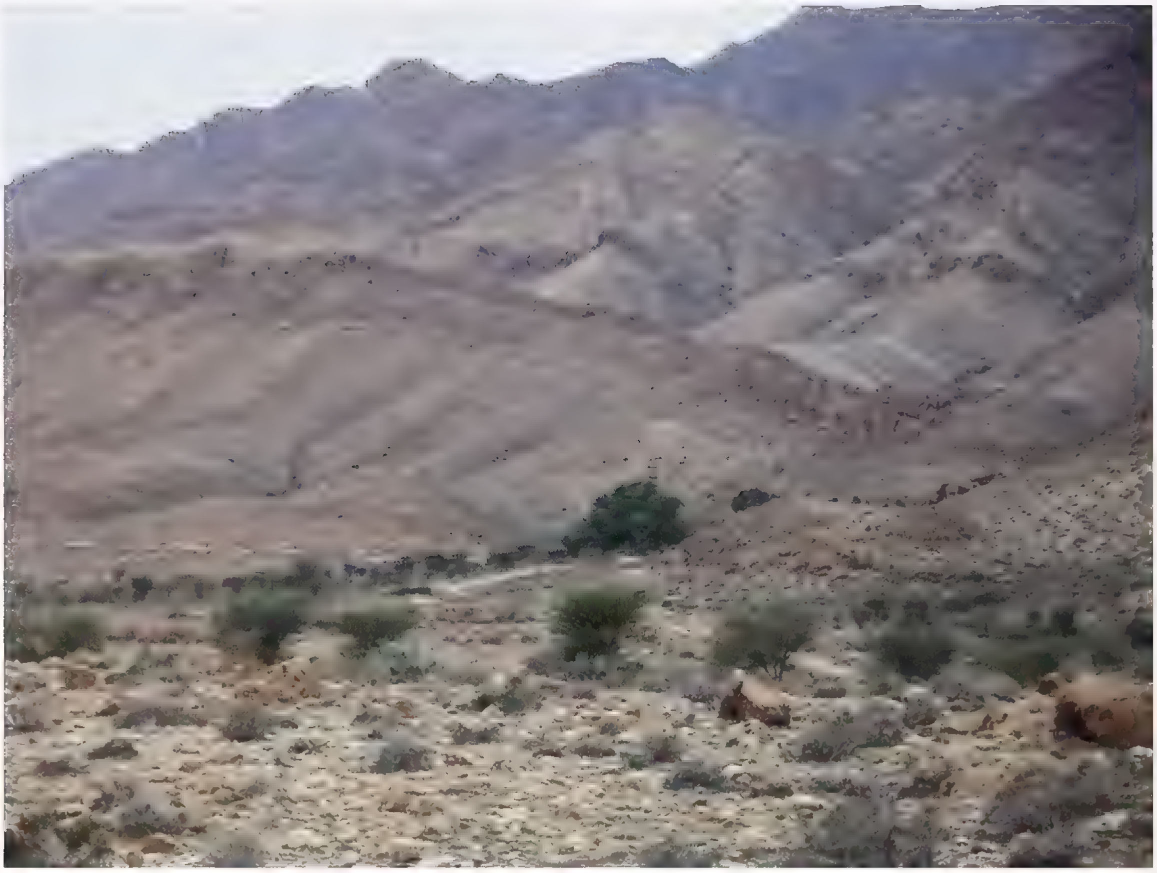

Fig. 10. Terra typica of *Tarentola fascicularis wolfgangi* ssp. n., Djebel Bou Hedma, Tunisia.

Habitat. Bou Hedma National Park is famous for its relict subtropical savanna with *Acacia tortilis raddiana* as the dominating tree. The climate is semi-arid, with variable amounts of rainfall (annual mean about 250 mm) in autumn and winter. On the pediments of Djebel Bou Hedma (Fig. 10) as well as on the slopes of the mountain chains to the west and south of it, *Tarentola fascicularis wolfgangi* ssp. n. is found in rock crevices, on walls and underneath of road bridges; the geckos are active at night.

Derivatio nominis. The species is dedicated to Wolfgang Böhme on the occasion of his retirement as the most successful German curator of herpetology after Robert Mertens. The senior author feels, however, also a strong affinity to the other Wolfgang, Wolfgang Bischoff, who retired this year, too. His field companionship in North Africa will be ever remembered.

Acknowledgements. We thank Sherif Baha El Din and Adel Ibrahim for providing Egyptian specimens, Wolfgang Bischoff for field companionship, Ulrich Willand for preliminary data, Miguel Vences and Susanne Hauswaldt for providing laboratory facilities.

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A new species of the genus *Tropiocolotes* from Central Saudi Arabia (Reptilia: Sauria: Gekkonidae)

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Abstract. A new species of the genus *Tropiocolotes* from central Saudi Arabia is described based on two specimens from the Ath-Thumamah region. The new species is a member of the subgenus *Tropiocolotes* and belongs to the clade including *T. steudneri* and *T. nattereri*.

Key words. *Tropiocolotes* sp. n., Ath-Thumama, Saudi Arabia.

INTRODUCTION

The genus *Tropiocolotes* Peters, 1880 comprises a group of small, nocturnal and ground dwelling geckos, rarely exceeding 35 mm snout-vent length. Biogeographically the distribution of these geckos follows a Saharo-sindian pattern, ranging from Morocco and Mauritania in the west to western India (Sindaco & Jeremčenco 2008; Agarwal 2009). About 13 nominal species are being distinguished within the genus *Tropiocolotes*, but in addition there are published records of specimens which would possibly deserve specific recognition and which are not yet formally described (Arnold 1980; Kordges 1998; Anderson 1999; Baha el Din 2001, 2006; Sindaco & Jeremčenco 2008). Beside this the species composition of the genus is under debate since the taxa of the eastern part of the distribution area are assigned to *Microgecko* Nikolsky, 1907 and *Asiocolotes* Golubev, 1984 on a generic or subgeneric level by some authors (Kluge 1983; Kuge 1991; Szcerbak & Golubev 1996; Sindaco & Jeremčenco 2008) while others treat all of those taxa as belonging exclusively to the genus *Tropiocolotes* (Anderson 1961, 1999). We prefer to follow the more inclusive interpretation of *Tropiocolotes* and use the name in the broader sense encompassing also the taxa of Iran, Afghanistan, Pakistan and India.

There have been uncertainties concerning the taxonomy of some of the African and Arabian taxa within the genus, like *T. tripolitanus algericus* Loveridge, 1947, *T. t. apoklomax* Papenfuss, 1969, *T. steudneri* (Peters, 1869) and *T. nattereri* Steindachner, 1901 (Baha el Din 1994, 2001; Werner 1998; Shifman et al. 1999). The main taxonomic issues were related to the validity of certain taxa (e.g., *T. t. apoklomax*; Baha El Din 2001), the taxonomic rank of certain taxa (e.g., *T. t. algericus* which was assigned specific rank based on a proven sympatric occurrence with *T. t. tripolitanus* Peters, 1880; Baha El Din 2001), species delimitation (e.g., between *T. nattereri* and *T. steudneri*, Shifman et al. 1999; the type material of both species is untraceable and therefore neotypes should be designated and a thorough rediscription of both taxa prepared) and to the existence of hitherto unknown species which were discovered recently (*T. nubicus* Baha El Din 1999, *T. bisharicus* Baha El Din 2001).

As already stated by Baha El Din (2001) the difficulty in finding and studying these diminutive animals, combined with their patchy geographical representation in scientific collections has led to a less than satisfactory taxonomic evaluation to date.

The specimens described as a new species in the present paper were collected in the Ath-Thumamah region in central Saudi Arabia, approximately 90 km northeast of Riyadh. According to Arnold (1986) the distribution of *Tropiocolotes* in Saudi Arabia is confined to north-western Saudi Arabia, but already Tilbury (1988) recorded it from the Riyadh area. Thus the first specimen from Ath-Thumamah collected by Kordges was not the first published record of the genus in central Arabia (contra Kordges 1998), but nevertheless the first record of the genus from Ath-Thumamah (contra Cunningham 2010, who listed *Tropiocolotes* as not yet confirmed for this area).

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MATERIAL

106 specimens of the genus *Tropiocolotes* from the collections of the Zoologisches Forschungsmuseum A. Koenig, Bonn (ZFMK), the Senckenberg Museum Frankfurt (SMF), the California Academy of Science (CAS) and the Natural History Museum Geneva (MHNG) belonging to *T. algericus* (n=14), *T. depressus* (n=3), *T. helenae* (n=10), *T. nattereri* (n= 14), *T. persicus* (n=12), *T. scortecci* (n=4), *T. steudneri* (n= 43), *T. tripolitanus* (n=4) and the new taxon described herein (n=2) were examined. For the species not available in the present study (*T. bisharicus*, *T. latifi*, *T. levitoni, T. nubicus*) morphological information were taken from Leviton & Anderson (1972), Szczerbak & Golubev (1996), Anderson (1999), Baha El Din (1999, 2001).

The following characters were collected from 59 specimens from Algeria, Egypt, Israel, Jordan and Saudi Arabia (belonging to *T. nattereri*, *T. steudneri* and the new taxon described herein): snout-vent-length, tail length (only intact tails), number and size of postmental scales, number of interorbitals (transverse scales across the interorbital region at mid orbits, excluding palpebral folds), number of upper and lower labials, number and characteristics of keels on subdigital lamellae, number and identity of scales bordering the nostril, number of scales around midbody. Beside this, data on colouration and pattern was collected. Additional data on morphological characters were taken from Baha el Din (1999, 2001) and Shifman et al. (1999). Measurements were taken with a digital caliper to the nearest 0.1 mm.

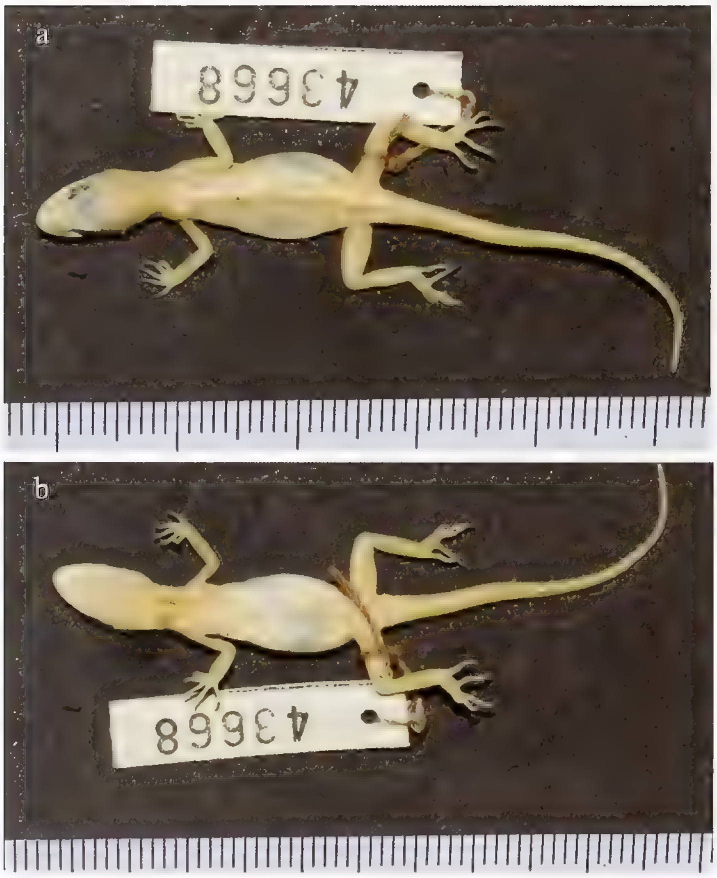

Fig. 1. Holotype of *Tropiocolotes wolfgangboehmei* sp. n. from Ath-Thumamah, Saudi Arabia (Fig. 1a: dorsal view, Fig. 1b: ventral view, Scale: 1mm interline distance).

Material examined

Tropiocolotes algericus**: Algeria:** SMF 8167, Algerian Sahara; **Mali:** MHNG 2678.087, north of Bombax; **Morocco:** MHNG 1553.065-067, Tarfaya; MHNG 993.027, Aouinet-Torkoz; SMF 73082-87, Goulimine; **Western Sahara:** MHNG 1545.076, El-Aioun. ***Tropiocolotes depressus*****: Pakistan:** SMF 64490-92, east of Chiltan-Mountains, Quetta. ***Tropiocolotes helenae*****: Iran:** MHNG 2627.011-16, MHNG 2641.100, MHNG 2646.056-058, Mehkuyeh. ***Tropiocolotes nattereri*****: Egypt:** MHNG 2710.017-018, Wadi Feran; SMF 8165, NW Sinai; ZFMK 70653-59, Ras Mohammed; **Israel:** SMF 47112, Wadi el Hedhira, Central Negev; **Jordan:** ZFMK 64673, Aqaba; **Saudi Arabia:** CAS 148526, Hagl [29 18 N; 34 57 E]; CAS 148616, Jabal as Sinfa [27 57 N; 35 47 E]. ***Tropiocolotes persicus*****: Pakistan:** SMF 63536-47, Hab Chauki. ***Tropiocolotes scortecci*****: Yemen:** MHNG 2428.065, Al Mabraz,Wadi Zabid; MHNG 2428.065, MHNG 2553.041, Mafraq-Mocca; MHNG 2581042, Sayhut. ***Tropiocolotes steudneri*****: Algeria:** CAS 138660-63, 3 km. East of Tamanrasset; ZFMK 19853, 15 km S Terhenanet; ZFMK 33839, 90km S In Salah; **Egypt:** CAS 156660, Maadi-Wadi Gindali Rd. [29 59 N, 31 28 E]; MHNG 2710.019-020, Oasis Kharga; SMF 22119, Kosseir; ZFMK 2359, ZFMK 64633, Luxor; ZFMK 20537, Cairo, Mokatana Hils; ZFMK 64641, ZFMK 64643, 10 km NW Cairo; ZFMK 65477, Giza Abu Rawash; ZFMK 77765-67, between Beni Suef u. Korimat; **Sudan:** CAS 174014, Assalaya Pump Station 3; MHNG 1186.078-079, Tabo; ZFMK 33840-59, Wadi Half; ZFMK 38429, Erkowit. ***Tropiocolotes tripolitanus*****: Egypt:** SMF 22472, Heliopolis; SMK 22473, Cairo; **Tunisia:** MHNG 1335.04, Tozeur; SMF 8166, Tunisian Sahara. ***Tropiocolotes* sp. n.: Saudi Arabia:** ZFMK 43668, ZFMK 87120, Ath-Thumama.

Despite the overall similarity of the taxa involved and the generally low level of character displacement, which is typical for geckoes, it became clear, that the specimens from central Saudi Arabia differ in several characters from all known taxa in the genus *Tropiocolotes* and will therefore be described as a new species.

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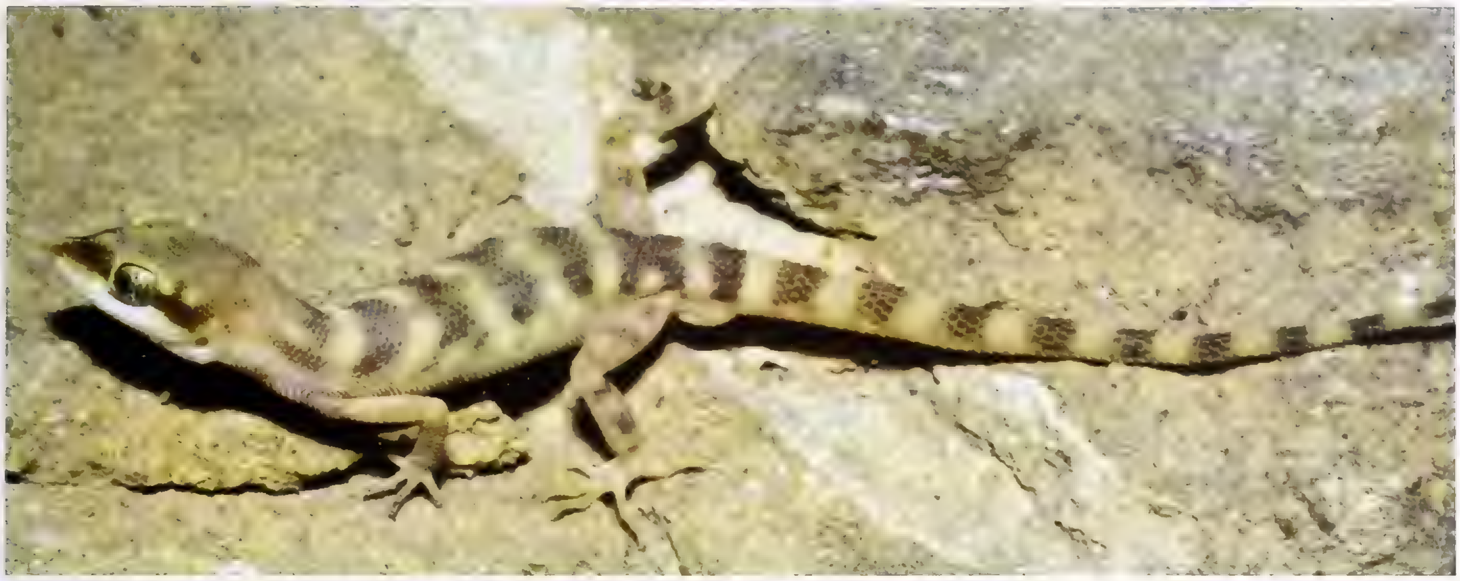

Fig. 2. Paratype of *Tropiocolotes wolfgangboehmei* sp. n. from Ath-Thumamah (25° 16’ N, 46° 37’ E), Saudi Arabia in life.

SPECIES DESCRIPTION

Tropiocolotes wolfgangboehmei sp. n.

Type material: Holotype, ZFMK 43668, Ath-Thumama, Saudi Arabia, leg. T. Kordges, 1985; Paratype, ZFMK 87120, Ath-Thumama (25° 16’ N, 46° 37’ E), Saudi Arabia, leg. T. Wilms, 09.05.2001, 10:30 hrs

Diagnosis. A small gecko with a maximum snout-vent-length of 29.4 mm. The species possesses all diagnostic characters of the genus *Tropiocolotes* (in the sense of Kluge 1967) including digits slightly angularly bent, not dilated, not fringed, not webbed, nor ornamented, covered below with a single series of transverse lamellae, pupil vertical, dorsal scales uniform, small, homogenous, imbricate to subimbricate, preanal and femoral pores usually absent.

Tropiocolotes wolfgangboehmei sp. n. has two pairs of postmental shields and therefore differs from *T. latifi* (no postmentals), *T. helenae* (one pair of postmentals) and *T. depressus* (no postmentals or only one pair of very small postmentals). From *T. persicus* it differs by having only four scales in contact with the nostril instead of five.

It differs from *T. algericus*, *T. tripolitanus*, *T. scorteccii*, *T. somalicus* and *T. bisharicus* by its smooth dorsal scalation. *T. wolfgangboehmei* sp. n. differs from *T. nattereri* by possessing clearly bi- or tricarinated subdigital scales (versus smooth subdigital scales) and from *T. steudneri* and *T. nubicus* by having two pairs of postmental shields of which the second is roughly a quarter of the size of the first (both pairs of roughly equal size in *T. steudneri* and *T. nubicus*).

Description of the Holotype. An adult female with intact tail. Body depressed. Snout-vent-length (SVL) 29.4 mm, Tail length 32.8 mm. Head narrow, 9.3 mm long (about 31.6 % of SVL). Neck distinct. Right limb 10.8 mm long. 5th digit of left manus lacking claw, all other digits complete. Tail 1.12 times SVL, cylindrical tapering evenly to its tip.

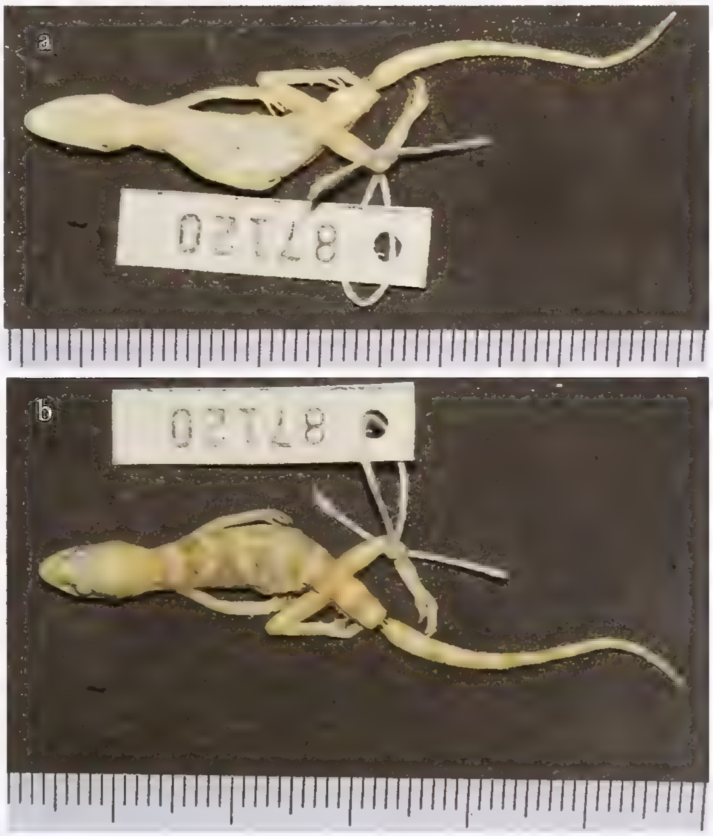

Fig. 3. Paratype of *Tropiocolotes wolfgangboehmei* sp. n. from Ath-Thumamah, Saudi Arabia (Fig. 3a: dorsal view, Fig. 3b: ventral view, Scale: 1 mm interline distance).

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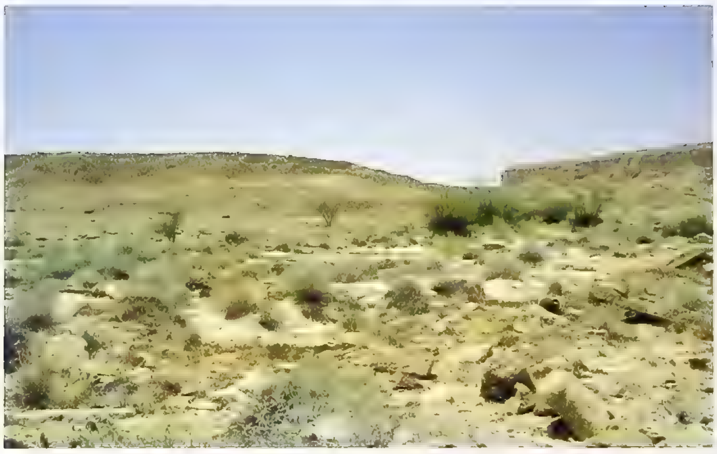

Fig. 4. Habitat and Paratype locality of *Tropiocolotes wolfgangboehmei* sp. n. at Ath-Thumamah (25° 16' N, 46° 37' E), Saudi Arabia.

Rostral 1.5 times as wide as high, divided partly by a median cleft. Nostril bordered by rostral, first upper labial and two small postnasals, which are separated by two large internasals. The internasals are followed by one pair of subequal scales. Snout and upper surface of the head covered by hexagonal scales which are juxtaposed. Loreal region covered with slightly swollen scales, which are somewhat smaller than the remaining scales on the head. 16 interorbitals, 10/10 upper labials, 8/8 lower labials. Occipitalregion covered by juxtaposed scales slightly smaller than the interorbitals, which become increasingly swollen in the neck. Mental slightly wider than rostral, pentagonal in shape extending posteriorly not to the level of the suture between first and second lower labials. One pair of large postmentals, in contact with mental and the first two lower labials. Second pair of postmentals only about one fourth the size of the first postmentals, separated from each other by four granular scales. The second pair of postmentals is in contact with the second lower labials.

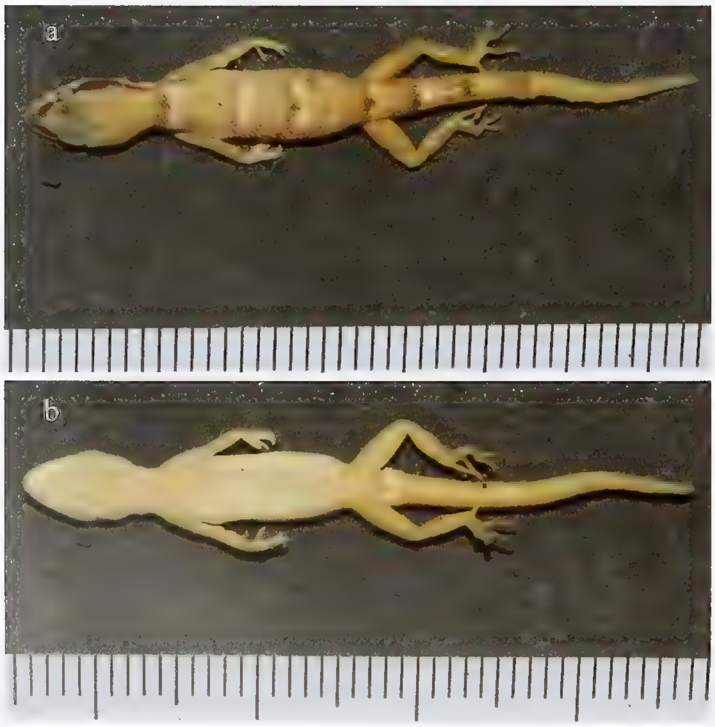

Fig. 5. *Tropiocolotes nattereri* (SMF 47112), Wadi el Hedhira, Central Negev, Israel (Fig. 5a: dorsal view, Fig. 5b: ventral view, Scale: 1mm interline distance).

Body scalation homogenous, scales imbricate and smooth. 58 scales around midbody. Chest widely opened by an incision. Dorsal sides of forelimbs covered with imbricate scales, scales of ventral sides juxtaposed and slightly swollen, somewhat smaller than scales on dorsal side of forelimbs. Dorsal and ventral sides of hind limbs covered with imbricate scales, which are almost equal in size. Posterior surface of thigh with smaller granular scales. Subdigital lamellae strongly bi- or tricarinate. Lamellar formula (digit 1 to 5) for left manus: 9, 12, 14, 13, 11.

Dorsal and ventral scales of the tail homogenous and imbricate. Scales at tail base not carinate, but becoming increasingly so distally. Postanal sacs weakly developed with two enlarged tubercular scales on either side. A pair of slightly enlarged preanal scales present.

Measurements (in mm, from preserved specimen): Snout-vent-length 29.4; tail length 32.8; head length 9.3; maximum head width 5.1; maximum head height 2.7; orbit diameter 2.0; distance orbit – snouth 3.2; distance orbit – ear 2.3; ear diameter 0.6.

Colouration of preserved specimen: The specimen is preserved in 70% ethanol and has almost completely lost his coloration and pattern. Kordges (1998) depicted this specimen in black and white, and its pattern resembles the paratype almost exactly (in having six dark transverse bands on the back and twelve on the tail, as well as having exactly the same pattern of the head).

Description of the Paratype. Paratype similar in most respects to holotype, except as noted. An adult male with intact tail, which was broken during preservation near the tail base. Body depressed. Snout-vent-length 27.3 mm, tail length 31.1 mm. Head narrow, head length 8.2 mm (about 30 % of SVL). Neck distinct. Right limb 9.3 mm long. All digits intact. Tail 1.13 times SVL, cylindrical tapering evenly to its tip.

15 interorbitals, 10/10 upper labials, 7/8 lower labials. Second pair of postmentals only about one fourth the size of the first postmentals, separated from each other by three granular scales. The second pair of postmentals is in full contact with the second lower labials, and almost reaches the third labial on the left.

Body scalation homogenous, scales imbricate and smooth. 59 scales around midbody, 66 scales between a well

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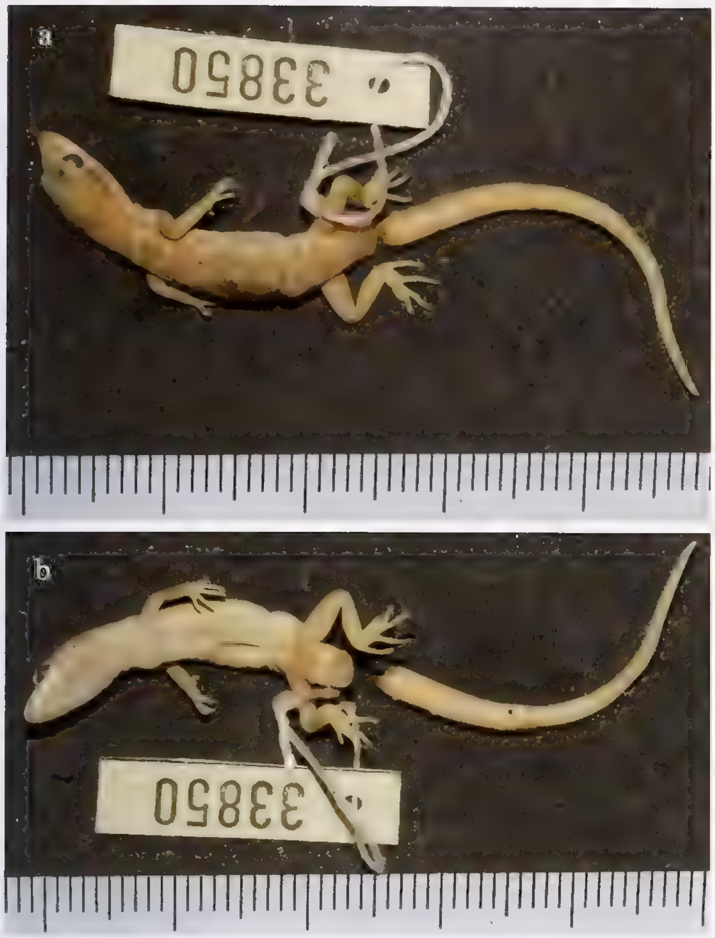

Fig. 6. *Tropiocolotes steudneri* (ZFMK 33850), Wadi Halfa, Sudan. (Fig. 6a: dorsal view, Fig. 6b: ventral view, Scale: 1mm interline distance).

marked interruption between throat and chest and cloacal slit. Dorsal sides of forelimbs covered with imbricate scales, some of which show very slight carination, scales of ventral sides juxtaposed and slightly swollen, somewhat smaller than scales on dorsal side of forelimbs. Lamellar formula (digit 1 to 5) for left manus: 9, 11, 15, 13, 10.

Measurements (in mm, from preserved specimen): Snout-vent-length 27.3; tail length 31.1; head length 8.2; maximum head width 4.9; maximum head height 2.9; orbit diameter 1.7; distance orbit – snouth 2.9; distance orbit – ear 2.0; ear diameter 0.7.

Colour in life: Head light brown with a broad dark brown band extending from the snout to just above the ear opening. A narrow yellow line extending axially from the rostral to the snout, up to the upper delimitation of the broad dark brown band. Palpebral fold yellow. Labials and underside of the head white. Dorsum light brown, with six broad, dark brown transverse bands. Colouration between those transverse bands yellowish brown. Ground colour of dorsal sides of limbs light brown. Hind limbs scattered with dark brown spots. Tail coloration light brown with ten dark brown transverse bands. Ventral side without any pattern, white.

Derivatio nominis. This species is named after Prof. Dr. Wolfgang Böhme in honour to his contributions to herpetology during his 39 years as curator of herpetology at the Zoological Research Museum A. Koenig, Bonn and as the academic mentor of two of the authors of the present paper.

Habitat. The holotype was found near a small village at the border of the Ath-Thumamah area (Kordges 1998). The paratype was found under a stone in a small canyon within the Buwayb-Escarpment which is a cretaceous coral reef consisting of sedimentary rock, mainly lime- and sandstone.

DISCUSSION

Tropiocolotes wolfgangboehmei sp. n. is known only from central Saudi Arabia. Because of the close proximity of Ath-Thumamah to the city of Riyadh we consider the *Tropiocolotes* recorded by Tilbury (1988) likely to be conspecific with this new taxon. Based on the external morphology *T. wolfgangboehmei* sp. n. is a member of the group consisting of *T. nattereri, T. steudneri* and *T. nubicus* and is most probably the sister taxon of *T. nattereri*. Biogeographically the distribution pattern of the *Tropiocolotes* of north-eastern Africa and Arabia is quite puzzling, not the least because of the involvement of at least two taxa which are not yet formally recognized (Guibé 1966, Arnold 1980, Anderson 1999). Due to the clarification on the taxonomic identity of *T. nattereri* and *T. steudneri* (Werner 1998, Shifman et al. 1999) and the description in the present paper, it is clear, that actually three nominal *Tropiocolotes* species are known to occur on the

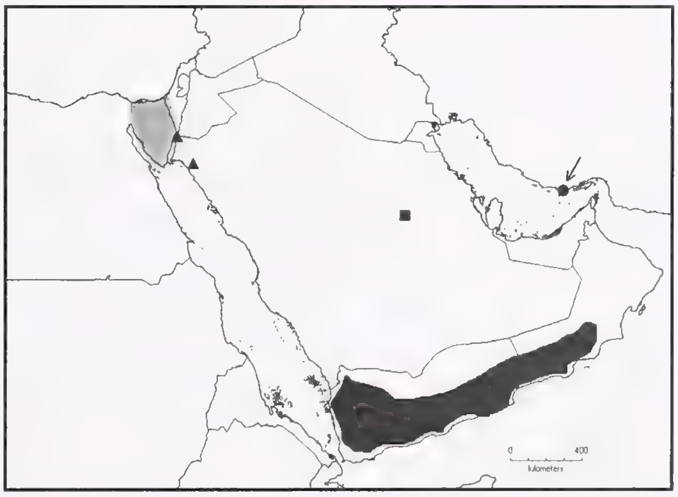

Fig. 7. Distribution of Arabian *Tropiocolotes*: ▲ *Tropiocolotes nattereri* from Saudi Arabia [upper ▲: CAS 148526, Hagl (29° 18' N; 34° 57' E); lower ▲ CAS 148616, Jabal as Sinfa (27° 57' N; 35° 47' E)], ■ *Tropiocolotes wolfgangboehmei* sp. n., ● *Tropiocolotes* spec. from Bandar-e-Lengeh (Anderson 1999), Iran; Black areas: approx. Distribution of *Tropiocolotes scortecci*, grey areas: approx. distribution of Tropiocolotes nattereri.

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Arabian Peninsula (*T. nattereri*, *T. wolfgangboehmei* sp. n. and *T. scortecci*). *T. nattereri* is known from north-western Saudi Arabia and the adjacent areas in Jordan, Israel and Egypt while *T. scortecci* is an endemic species of southern Arabia (Oman and Yemen). *T. wolfgangboehmei* sp. n. is the only species distributed in central Arabia some 800–1000 km away from the nearest *Tropiocolotes* localities in north-western Saudi Arabia, Oman/Yemen and Iran.

In the past, several authors (Tilbury 1988, Schneider 1990, Baha El Din 2006, Cunningham 2010) assigned the central Arabian *Tropiocolotes* to *T. steudneri* or *T. nattereri*. Two specimens from Bandar-e Lengeh on the coast of the Arabian/Persian Gulf in Iran were also tentatively assigned to *T. steudneri* (Guibé 1966, Anderson 1999). Based on the current distribution of *Tropiocolotes* it would zoogeographically be extremely unlikely that the Iranian specimens belong to either *T. steudneri* or *T. nattereri*. Based on the morphological data given by Guibé (1966) and Anderson (1999) and the photograph given by Anderson (1999) we are sure that these animals do not belong to *T. wolfgangboehmei* sp. n. but to a new, as yet undescribed taxon. Baha El Din (2001) suggested the investigation of the relationship of those Iranian specimens to two *Tropiocolotes* from eastern Dhofar, Oman, which were tentatively assigned to *T. scortecci* by Arnold (1980) despite notable differences from *T. scortecci* specimens from further west in Dhofar and from the type locality of this taxon in Hadramaut, Yemen. The taxonomy of the genus *Tropiocolotes*, especially in Arabia, is still in need of a thorough revision, not only to clarify the species composition within the genus but also to gain more data on the distribution of the respective taxa and to establish a hypothesis on their phylogenetic relationships.

Acknowledgements. We thank H.H. Prince Bandar ibn Saud (Director General, Saudi Wildlife Commission, Riyadh) for the support and continuous interest in our herpetological studies in Saudi Arabia. The study would not have been possible without the help of many colleagues of which we would like to thank H.E. Prof. Dr. A. H. Abuzinada (former Director General, NCWCD, Riyadh), Prof. Dr. I. Nader (Former Director of KKWRC, Thumama), and Dr. I. Galal (Riyadh). For the loan of important material we thank Prof. Dr. W. Böhme (ZFMK, Bonn), Dr. A. Schmitz (MHNG, Geneva), J. Vindum (CAS, San Francisco) and Dr. G. Köhler (SMF, Frankfurt).

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Description of a new subspecies of *Kinyongia uthmoelleri* (Müller, 1938) (Squamata: Chamaeleonidae) with notes on its captive propagation

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Abstract. A new population of *Kinyongia uthmoelleri* was found in the South Pare Mountains in Tanzania in 2000 by J. Mariaux of the Natural History Museum of Geneva (MHNG). The morphology of this population corresponds well with that of other previously known populations of *K. uthmoelleri* from Mt. Hanang and the Ngorongoro crater highlands. Specimens from South Pare and Ngorongoro are morphologically very similar and show some distinctive characters which are divergent from the holotype of *K. uthmoelleri* and other specimens from Mt. Hanang: smaller size, smooth squamation on head and body, smooth head crests, clearly bi-forked parietal crest (only in males), parietal crest composed of only a single row of scales, a relatively narrower and longer head and no sexual dimorphism in the tail length. *K. uthmoelleri* is known from only few museum specimens but these morphological differences and geographic isolation justify describing the Ngorongoro and South Pare populations as a new subspecific taxon: *Kinyongia uthmoelleri artytor* nov. ssp. The new subspecies has been successfully kept and bred in captivity by one author, and a short description is given of its captive maintenance.

Key words. *Kinyongia uthmoelleri*, new subspecies, South Pare Mountains, captive propagation.

INTRODUCTION

Despite several recently described *Kinyongia* taxa from East Africa (Menegon et al. 2009; Necas 2009; Necas et al. 2009) the diversity within this genus has not yet been completely uncovered. Several publications covering material from the Eastern Arc Range have contributed to knowledge on the systematics and taxonomy of these chameleons (Mariaux et al. 2008; Tilbury et al. 2006). The type material of the taxon described in the present paper was collected in 2000 and was at that time deposited under the name "*Bradypodion tavetanum*" in the Muséum d'histoire naturelle (MHNG) in Geneva.

Kinyongia uthmoelleri was described by Müller (1938) as *Chamaeleo uthmölleri* on the basis of a single specimen from Mt. Hanang. This specimen was collected at 2300 m asl in montane forest. In Loveridge's (1957) check list of East African reptiles and amphibians he designated *uthmoelleri* as a subspecies of *Ch. fischeri*, a two-horned species. Mertens (1966) followed this classification, despite the fact that he treated it as a full species in an earlier publication after discovering the second specimen known to science in the Staatliches Museum für Naturkunde Stuttgart (SMNS) (Mertens 1955). On the basis of lung and hemipenial morphology Klaver & Böhme (1986) recognized *uthmoelleri* as a full species and included it in the genus *Bradypodion*. Böhme & Klaver (1990) discovered a third specimen, the first recorded female of this species, in the Royal Museum for Central Africa in Tervuren (MRAC). The above mentioned second and the third specimens were collected from the locality of Oldeani in the Ngorongoro crater highlands, a massif several hundred kilometres north of the type locality on Mt. Hanang. Price (1996) also mentions statements from local people about locations between Babati and Singida (a road that passes close to Mt. Hanang) and 72 km northeast of Mt. Hanang but up til now the presence of *K. uth-*

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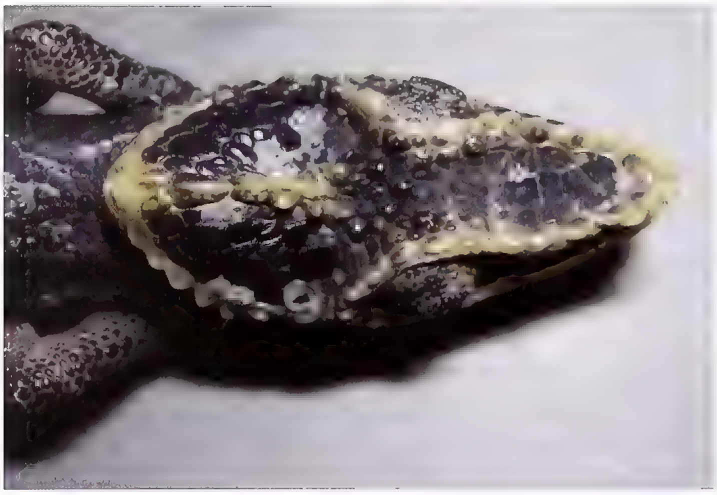

Fig. 1. Head view of the holotype of *K. u. uthmoelleri* (photo: G. Vogel).

moelleri at these locations have not been confirmed. Recently the taxon *uthmoelleri* was placed with all other east African *Bradypodion* in a new genus, *Kinyongia* (Tilbury et al. 2006). In the last 15 years only two authors have published details on the captive husbandry and breeding of *K. uthmoelleri*, specimens collected from the Ngorongoro crater highlands (Price 1996; Necas & Nagy 2009). Around the year 2000, specimens of "*Bradypodion uthmoelleri*" appeared in the international pet trade. These animals were very small in overall size, more slender and with smoother scalation than *K. uthmoelleri* specimens from Mt. Hanang. Even after six years of keeping some of these specimens in captivity these distinct characters have not changed and so ontogenetic change in these characters can be ruled out. Unfortunately, the geographic origin of these specimens was not known until four similar specimens were discovered in the collection of the Muséum d'histoire naturelle in Geneva in 2004, which suggests they originate from the same locality, the South Pare Mountains, and belong to the new subspecies described in this paper.

MATERIAL AND METHODS

In total 20 specimens of *K. uthmoelleri* of both subspecies with a confirmed collection locality were located in museum collections and investigated: 8 from Mt. Hanang (5 males [ZSM 1/1948 (Holotype), ZFMK 74955, ZFMK 82188 and ZFMK 82189], 3 females [ZFMK74953, ZFMK 74954 and ZFMK 82191] and one subadult [ZFMK 82190]), 8 from the Ngorongoro crater highland area [1 male (SMNS 324), 2 females (ZFMK 58664 and ZFMK 58665), 1 subadult (MRAC R.G. 21852), 4 embryos (ZFMK 58666-69] and 4 from the South Pare Mountains [2 males (MHNG 2612.65 and MHNG 2612.66), 1 female (MHNG 2612.67), 1 juvenile (MHNG 2612.64)]. It seems probable that the embryos in the ZFMK collection are the unhatched specimens reported by Price (1996).

Head-body length (HBL), tail length (TL), total length (ToL), head length (HL) and head width (HW) were measured in all specimens except in the embryos. The data of MRAC R.G. 21852 were taken from Böhme & Klaver (1990). The ratio of HL to HW and the percentages of HL to HBL, TL to ToL and TL to HBL were calculated. In addition, we recorded head crest morphology following Necas (1994), and the morphology and pattern of body scalation.

RESULTS

All measurements and investigated morphological characters of the specimens are listed in Tables 1–3. The morphological traits which differentiate the male specimens of Mt. Hanang from those of the South Pare Mountains and Ngorongoro crater highlands are: higher measurements, a relatively broader and shorter head, rougher (more convex) scalation on the head and body, canthus parietalis (cp) not bi-forked anteriorly but fan-shaped anteriorly and the cp composed of two rows of scales (Fig.

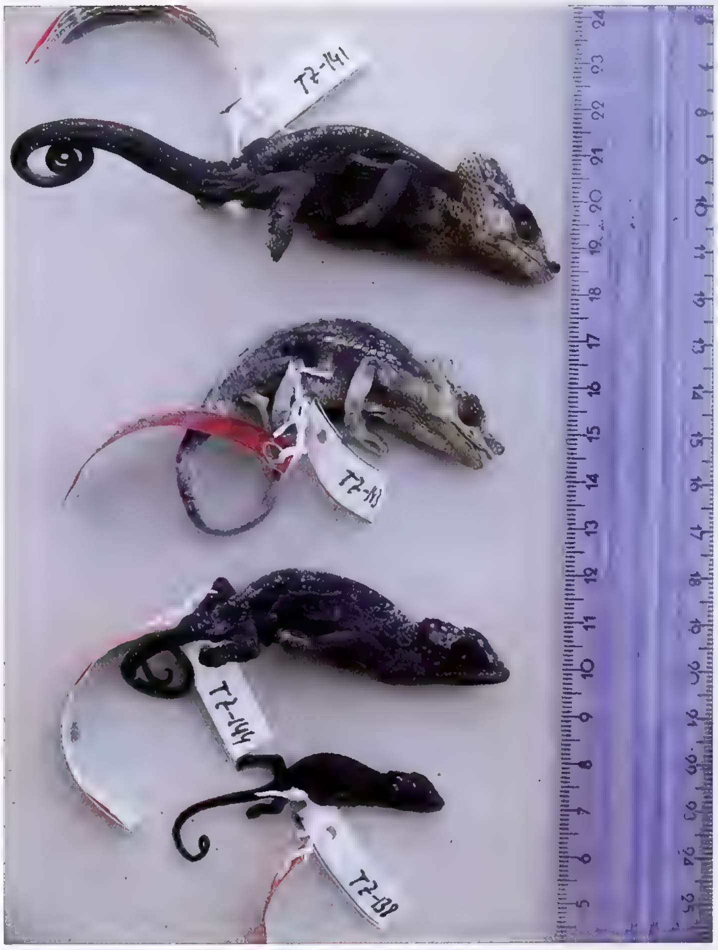

Fig. 2. Type material of *K. u. artytor* ssp. n. (photo: G. Vogel).

Table 1. Morphological measurements of *K. uthmoelleri* in mm.

specimen	locality	sex	HBL	TL	ToL	HW	HL	remark
ZFMK 74955	Mt. Hanang	m	90.1	122.8	212.9	15.1	26.6	
ZFMK 82188	Mt. Hanang	m	85.2	119.6	204.6	15.8	26.0	
ZFMK 82189	Mt. Hanang	m	92.8	125.7	218.5	16.4	30.0	
ZFMK 82190	Mt. Hanang	m	69.9	93.1	163.0	12.0	22.7	subadult
ZSM 1/1948	Mt. Hanang	m	93.0	134.0	227.0	16.0	32.0	holotype of *K. u. uthmoelleri*
SMNS 324	Ngorongoro area	m	83.0	116.0	199.0	13.0	31.0	
MHNG 2612.64	South Pare Mountains	m	40.0	46.0	86.0	6.5	13.5	juvenile; paratype of *K. u. artytor* ssp. n.
MHNG 2612.65	South Pare Mountains	m	80.0	100.0	180.0	13.0	31.0	holotype of *K. u. artytor* ssp. n.
MHNG 2612.66	South Pare Mountains	m	67.0	86.0	153.0	10.0	24.0	paratype of *K. u. artytor* ssp. n.
ZFMK 74953	Mt. Hanang	f	86.1	95.3	181.4	13.2	20.2	
ZFMK 74954	Mt. Hanang	f	82.0	91.5	173.5	13.5	24.1	
ZFMK 82191	Mt. Hanang	f	78.5	82.9	161.4	12.9	21.3	
ZFMK 58664	Ngorongoro area	f	78.6	95.1	173.7	11.4	21.1	
ZFMK 58665	Ngorongoro area	f	76.1	92.2	168.3	12.2	21.0	
MRAC R.G.21852	Ngorongoro area	f	54.0	61.0	115.0	8.0	19.0	subadult
MHNG 2612.067	South Pare Mountains	f	70.0	81.0	151.0	10.0	21.0	paratype of *K. u. artytor* ssp. n.

1). The females show the same differences between both populations except that the females from the Mt. Hanang population show also a fan-shaped cp anteriorly, instead of no furcation at all in the females from the South Pare Mountains and Ngorongoro highlands. Additionally, the Mt. Hanang specimens are sexually dimorphic in tail length relative to body length (males having relatively longer tails than females), whereas relative tail length between the sexes of specimens from the South Pare Mountains and Ngorongoro highlands specimens is more or less the same. Based on these key characters that differentiate the two groups, we describe the populations from the South Pare Mountains and the Ngorongoro crater highlands as a new subspecific taxon.

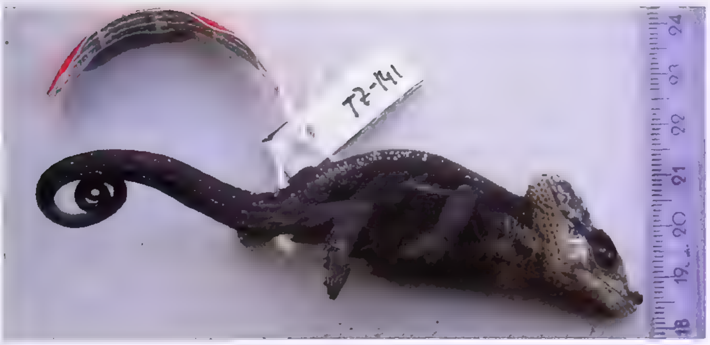

Fig. 3. Holotype of *K. u. artytor* ssp. n. (photo: N. Lutzmann).

Kinyongia uthmoelleri artytor ssp. n.

We chose the syntopic specimens collected by J. Mariaux & C. Vaucher in the South Pare Mountains during their journey in 2000 as the type specimens (Fig. 2).

Diagnosis. A small chameleon, which differs from the nominate form on Mt. Hanang in the following characters: less convex scalation on body and head, smooth head crests, parietal crest distinctly bi-forked anteriorly, the ridge of the parietal crest contains only one scale row, a higher ratio of HL to HW and HL to HBL (relatively longer and narrower heads), smaller total length [153.0–199.0 mm in males (204.6–227.0 mm in *K. u. uthmoelleri*) and 151.0–173.7 mm in females (161.4–181.4 mm in *K. u. uthmoelleri*)] and no sexual dimorphism in the relative tail length.

Description of the Holotype (Figs 3–5). MNHG 2612.65, adult male, 1840 m asl, South Pare Mountains, North Tanzania, leg. J. Mariaux & C. Vaucher, 29. 09. 2000. HBL 80.0 mm, TL 100.0 mm, ToL 180.0 mm, HL 31.0 mm, HW 13.0 mm, the belly is cut and the intestine removed, both hemipenes are partly everted, length of lower jaw 21.0 mm, distance from front edge of eye to nostril 9.8 mm, distance from nostril to snout tip 5.4 mm, distance from lower jaw to the tip of casque 7.5 mm, head width between eyes 6.5 mm, canthus temporalis from eye to angle 7.7 mm, canthus parietalis (cp) is bi-forked anteriorly (Fig. 5), distance from bifurcation of cp to the top of

Table 2. Ratios of morphological measurements of *K. uthmoelleri.*

specimen	location	sex	HL/HW	HL as % HBL	TL as % ToL	TL as % HBL
ZFMK 74955	Mt. Hanang	m	1.76	29.52	57.68	136.29
ZFMK 82188	Mt. Hanang	m	1.65	30.52	58.46	140.38
ZFMK 82189	Mt. Hanang	m	1.83	32.33	57.53	135.45
ZFMK 82190	Mt. Hanang	m	1.90	32.47	57.12	133.19
ZSM 1/1948	Mt. Hanang	m	2.00	34.41	59.03	144.09
SMNS 324	Ngorongoro area	m	2.38	37.35	58.29	139.76
MHNG 2612.064	South Pare Mountains	m	2.08	33.75	53.49	115.00
MHNG 2612.065	South Pare Mountains	m	2.38	38.75	55.56	125.00
MHNG 2612.066	South Pare Mountains	m	2.40	35.82	56.21	128.36
ZFMK 74953	Mt. Hanang	f	1.53	23.46	52.54	110.69
ZFMK 74954	Mt. Hanang	f	1.79	29.39	52.74	111.59
ZFMK 82191	Mt. Hanang	f	1.65	27.13	51.36	105.61
ZFMK 58664	Ngorongoro area	f	1.85	26.84	54.75	120.99
ZFMK 58665	Ngorongoro area	f	1.72	27.60	54.78	121.16
MRAC R.G.21852	Ngorongoro area	f	2.38	35.19	53.04	112.96
MHNG 2612.067	South Pare Mountains	f	2.1	30.00	53.64	115.71

casque 13.1 mm, length of bifurcation of cp 4.4 mm, maximum width of bifurcation of cp 4.3 mm, one conical scale in the neck smaller than 2.0 mm, no ventral or tail crests, collection and field number (TZ-141) are tied around the left hind leg. The scales on the head, the head crests and the body are flat. Only the ridge of the cp is pronounced though not denticulate. Fig. 6 shows the colouration of the holotype in life.

Variation on the paratypes (MNHG 2612.64, 2612.66-67). All measurements of the paratypes and the other specimens of *K. u. artytor* ssp. n. are shown in Tables 1–2. MNHG 2612.64 is a juvenile male, the belly is cut and the intestines are removed, the colouration after preservation is very dark, collection and field number (TZ-138) is tied around the right hind leg. MNHG 2612.66 is an adult male and fits quite well with the description of the holotype: belly is cut but the intestines are still present, 2 conical scales in the neck, collection and field number (TZ-143) are tied around the right hind leg. The original colouration is better preserved: head is greyish, red radiations on the eyes, which continue darker on the head sides, the interstitial skin is red around throat and neck, the lateral stripe is greyish on dark background, the tail is greyish. MNHG 2612.67 (Fig. 7) is an adult female with a flat casque, cut belly without intestines and one conical scale in the neck. Collection and field number (TZ-144) are tied around the left hind leg, the colouration after preservation is very dark with only some greyish flat scales on the head and body.

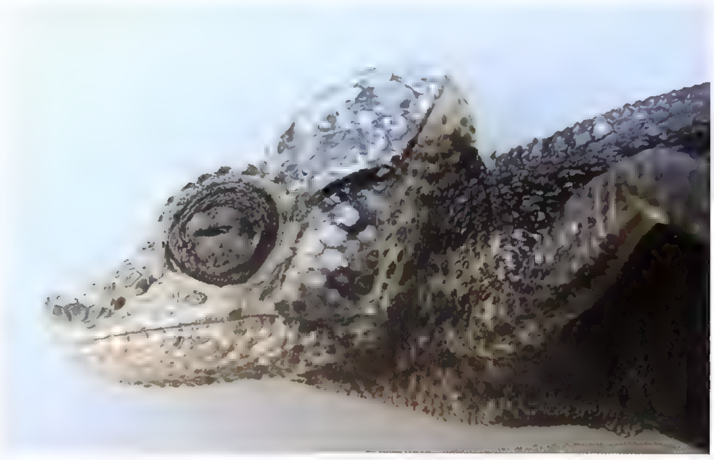

Fig. 4. Portrait of the holotype of *K. u. artytor* ssp. n. (photo: N. Lutzmann).

Distribution. *K. u. artytor* ssp. n. is know only from the South Pare Mountains and the Ngorongoro crater highlands (Fig. 8).

Etymology. The subspecies name "*artytor*" is the latinised substantive of the Greek verb "αρτυειν" (artyein), which can be translated as "to prepare / to make ready requiring skills". We name this new subspecies in honour and tribute to Prof. Dr. Wolfgang Böhme and his skills to prepare dozens of students on their way to scientific careers, which was also the case for four of the authors of this publication.

Captive maintenance. All specimens were kept individually in full gauze terrariums indoor and outdoor in the same cages in order to minimize the stress of relocation. The size of the terrariums were for females 50x50x80 cm and for males 45x50x70 cm (length x width x height). All specimens were kept outdoor from spring to autumn, if the temperatures did not fall consistently below 10 °C at night time. The highest recorded temperature was 35 °C at noon, the lowest 5 °C at night time. The cages were exposed to the sun in the morning and fell into shade around

Table 3. Morphological characters of *K. uthmoelleri*.

specimen	location	sex	head scalation	body scalation	bi-forked cp	No. scale rows on the ridge of cp
ZFMK 74955	Mt. Hanang	m	rough	rough	no	2
ZFMK 82188	Mt. Hanang	m	rough	rough	no	2
ZFMK 82189	Mt. Hanang	m	rough	rough	no	2
ZFMK 82190	Mt. Hanang	m	rough	rough	no	1–2
ZSM 1/1948	Mt. Hanang	m	rough	rough	no	2
SMNS 324	Ngorongoro area	m	flat	flat	yes	1
MHNG 2612.065	South Pare Mountains	m	flat	flat	yes	1
MHNG 2612.066	South Pare Mountains	m	flat	flat	yes	1
ZFMK 74953	Mt. Hanang	f	rough	rough	no	2
ZFMK 74954	Mt. Hanang	f	rough	rough	no	2
ZFMK 82191	Mt. Hanang	f	rough	rough	no	2
ZFMK 58664	Ngorongoro area	f	flat	flat	–	1
ZFMK 58665	Ngorongoro area	f	flat	flat	–	1
MRAC R.G.21852	Ngorongoro area	f	flat	flat	?	?
MHNG 2612.067	South Pare Mountains	f	flat	flat	–	1

noon. In spring and autumn the cages were sprinkled with water four times per day (in midsummer 6 times) for up to four minutes in the hottest time of the day. During the winter the terrariums were illuminated with common terrarium-tubes (T5 with 35 W) 13 hours per day. A halogen spot was activated for 45 minutes three times per day for basking, so that the ambient temperature stayed between 22 and 24 °C at day time and between 6 and 16 °C at night time. The terrariums were completely sprinkled with water in the morning and evening. The diet consisted of small arthropods, mainly self-bred crickets, grasshoppers, flies, cockroaches etc. Every second feeding the food was enriched with vitamins and minerals. Only pregnant females were additionally given small pieces of cuttlebone. To trigger mating behaviour, the males were transferred into the cages of the females. Immediately, the males started head bobbing and displayed bright colours. In all cases the females displayed a colouration of greenish-white with small black dots, whereon the males stopped courtship. Matings have not be observed until now, but after several days the females started gaining weight and became visibly rounder. The males were subsequently removed, because it seemed that the females only lay their eggs if there were no males in their vicinity. Older females laid their clutches without test excavations, younger females with test excavations at a depth of 5 to 7 cm into the terrarium substrate. The clutches consisted of 7 to 12 eggs. The dimensions of the eggs were approximately 8.0x4.0 mm. The eggs were incubated in completely closed, small plastic boxes in wet vermiculite. After approximately 115 days at 19–21 °C during the day and 15–18 °C at night, the temperatures were increased to 22 °C during the day and 20 °C at night. At this time the humidity of the vermiculite was also increased to simulate the beginning of a rainy season. Hatching started after 147 to 161 days. After the hatchlings opened the egg shells, they occasionally paused for up to 3 days to resorb the yolk. The young chameleons were kept individually in smaller cages 25x25x40 cm under the same conditions as the adults. It should be taken into account that the temperature changes should not be as pronounced for the juveniles as for the adults, because it seems that they are unable to thermoregulate effectively. The maximum recorded lifespan in captivity for this species is six years (Fig. 9).

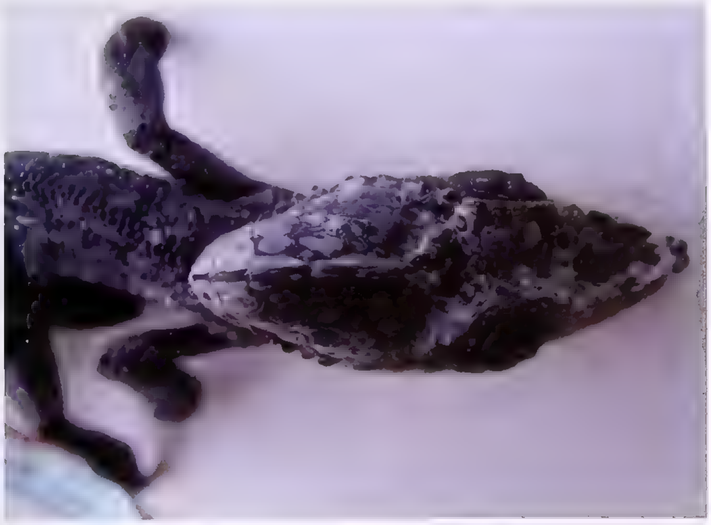

Fig. 5. Head view of the holotype of *K. u. artytor* ssp. n. (photo: N. Lutzmann).

DISCUSSION

The genus *Kinyongia* contains currently 17 species, all of which are restricted to moist montane forests in the East and Central African highlands. Recently several new

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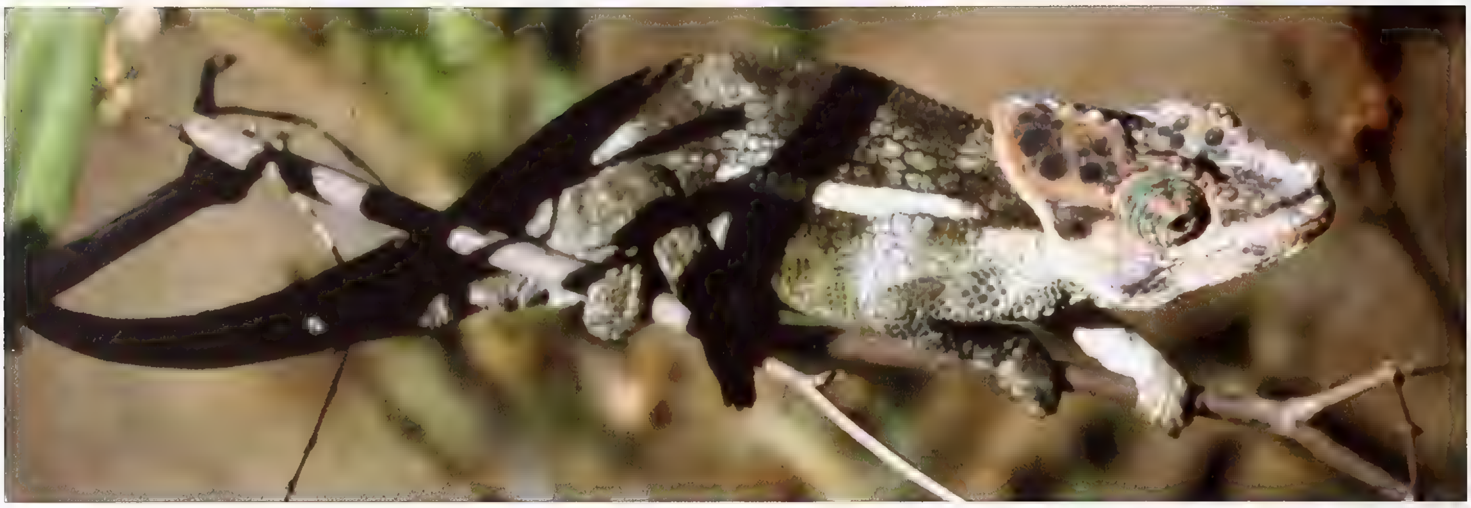

Fig. 6. Holotype of *K. u. artytor* ssp. n. in life (photo: J. Mariaux).

species have been described from montane forests in Kenya and Tanzania (Menegon et al. 2009, Necas 2009, Necas et al. 2009) and several subspecies have also been raised to species status based on genetic divergence and detailed morphological studies (Mariaux et al. 2008). No doubt more species remain to be discovered in the still poorly surveyed mountain ranges across East Africa. The discovery of *K. uthmoelleri* in the South Pare Mountains also shows that species' distribution ranges are not well documented and it is quite likely that *K. uthmoelleri* also occurs on other massifs in-between these now known populations, such as Mt. Kilimanjaro and Mt. Meru (Fig. 8). *K. uthmoelleri* has a similar distribution to the *Trioceros sternfeldi* species complex, including the recently described *T. hanangensis* (Krause & Böhme 2010). Although the phylogeography of all *T. sternfeldi* populations has not been investigated, the Mt. Hanang population has been identified as a divergent sister clade to the Mt. Meru/ Kilimanjaro populations. A similar pattern is found in *K. uthmoelleri*, the Mt. Hanang populations morphologically divergent from the Ngorongoro/ Pare populations, suggesting that despite its geographically intermediate position, Mt. Hanang populations have been isolated for a longer period of time. Volcanic activity in the North of Tanzania, which created these massifs, persisted from Oligocene (37 myr ago) to the Quaternary. Subsequent colonisation and population fragmentation of chameleon populations on these massifs has resulted in their diversification into a number of morphologically similar but clear divergent (sub-) species.

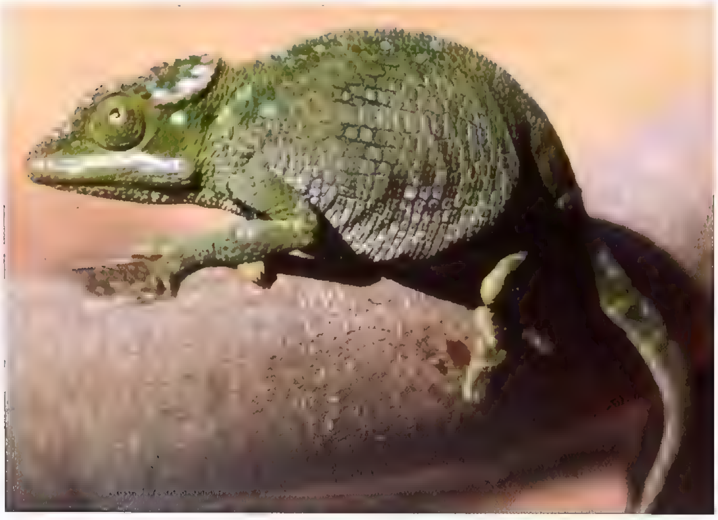

Fig. 7. Female paratype of *K. u. artytor* ssp. n. in life (photo: J. Mariaux).

The rarity of some species of the genus *Kinyongia* in museum collections is explainable because they inhabit the rainforest canopy and their cryptic morphology and behaviour (Necas & Nagy 2009). Unfortunately *Kinyongia uthmoelleri* is one of the rarest chameleons of East Africa in museum collections, although Price (1996) mentioned, that this species is common in the Ngorongoro crater highlands. But during eight days of fieldwork he also found only five specimens. In total, there are only 20 specimens in museum collections in Europe from three different localities and more intensive fieldwork is required to bring to light if this reflects the real situation of population densities, distribution and ecology of this species in the wild. Further collections will also confirm if the morphological variation recorded here, from the relatively few specimens available, is consistent within and between the three populations.

Nevertheless, there are pronounced morphological differences between the Ngorongoro and South Pare specimens and the specimens from the type locality on Mt. Hanang (Müller 1938). These are sufficiently distinct to justify their description as a new taxon. This is similar to the situation where *K. boehmei* was originally described as a subspecies of *K. tavetana* (Lutzmann & Necas 2002) and later elevated in to full species rank based on genetic divergence from all other two-horned chameleons (Mariaux

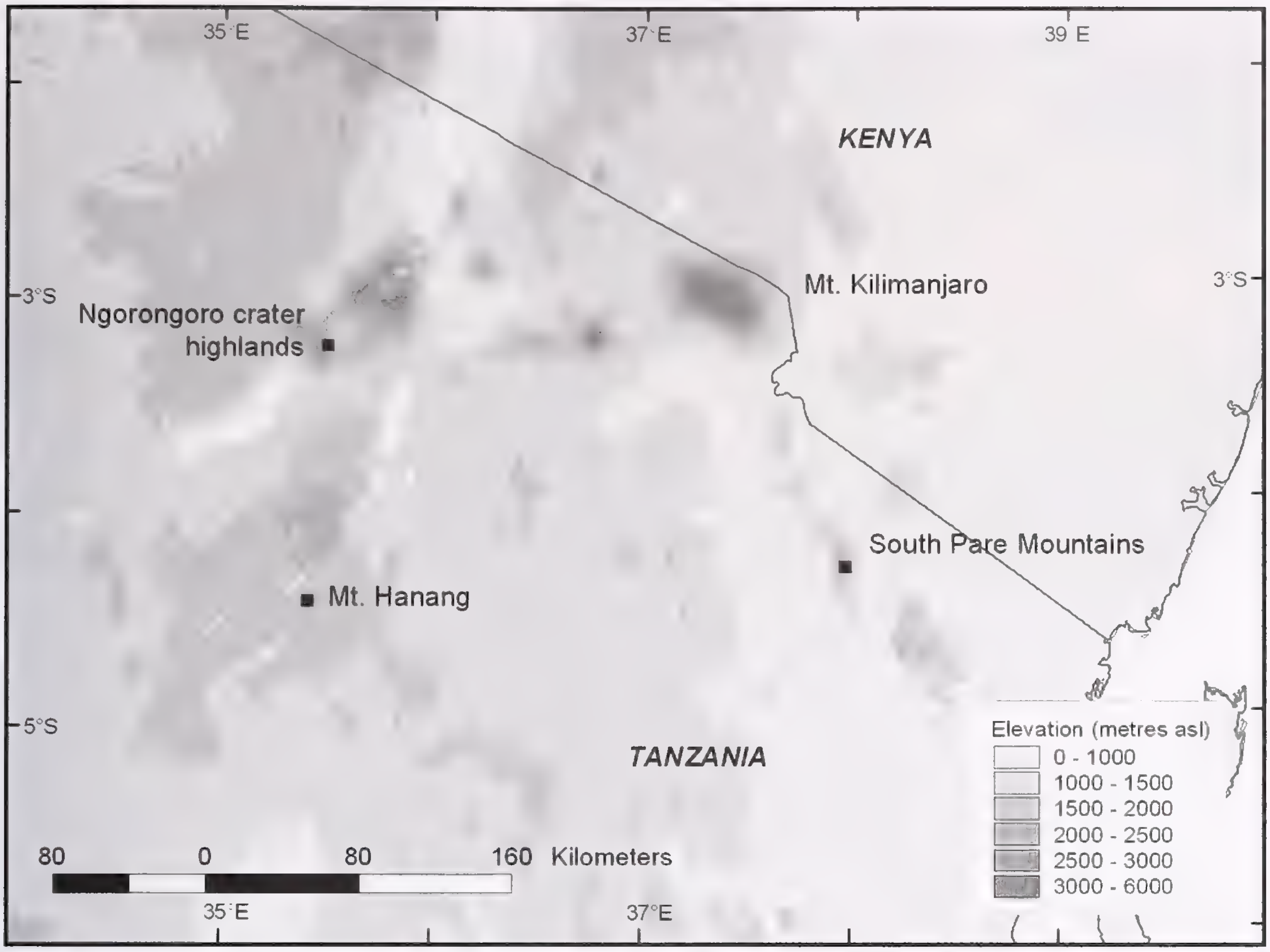

Fig. 8. Collecting localities of *K. uthmoelleri* [*K. u. uthmoelleri* (Mt. Hanang); *K. u. artytor* ssp. nov. (South Pare Mountains and Ngorongoro crater highlands)].

et al. 2008). Molecular studies have revealed numerous cryptic species among East African chameleons (Matthee et al. 2004; Tilbury & Mariaux 2006; Mariaux et al. 2008, Krause & Böhme 2010) and follow-up studies using molecular data should provide a better insight into the evolutionary relationships and genetic divergence that exists between the three isolated populations of *K. uthmoelleri*, some of which may justify species status.

Acknowledgements. We specially want to thank Jean Mariaux, Geneva, for providing us the with type material, information on the type locality and pictures of this new taxon. Thanks also to the colleagues providing acces to collection and material: Wolfgang Böhme and Ulla Bott (ZFMK), Frank Glaw (ZSM), Andreas Schlüter and Axel Kwet (SMNS).

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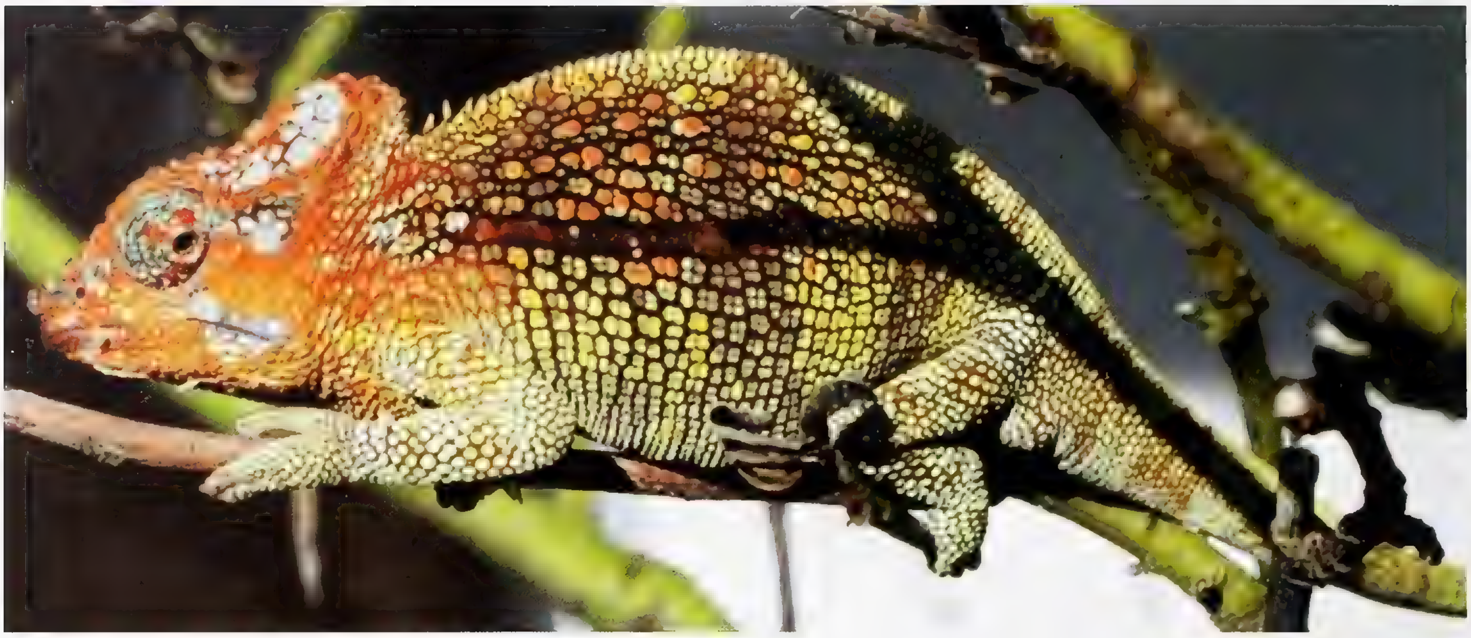

Fig. 9. A six year old *K. u. artytor* ssp. n. in captivity (photo: R. Lademann).

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A new species of the genus *Lycodon* (Boie, 1826) from Yunnan Province, China (Serpentes: Colubridae)

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Abstract. A new species of the genus *Lycodon* is described from Yunnan Province, People's Republic of China. It differs from the superficially similar *Lycodon fasciatus* by the fact that the loreal is not entering orbit, in colouration, and lower numbers of subcaudals and infralabials. From the *Lycodon ruhstrati* group it differs by the colouration of the venter and the dorsal bands. This new species is only known the Chinese province of Yunnan.

Keywords. Oriental Region, China, Colubrinae, *Lycodon fasciatus*, taxonomy, *Lycodon synaptor* sp. n.

INTRODUCTION

Snakes of the species rich genus *Lycodon* Boie, 1826 received considerable attention in most regions of Asia. Six new species were described form the Philippines (Ota & Ross 1994; Lanza 1999; Gaulke 2002) and new species were discovered in Cambodia (Daltry & Wüster 2002), India (Mukherjee & Bhupathy 2007) and Myanmar (Slowinski et al., 2001). The taxonomy of the Chinese part of the genus remained unattended until recently. Pope (1935) listed five species, namely *Lycodon capucinus* Boie, 1827, *Lycodon fasciatus* (Anderson, 1879), *Lycodon laoensis* Günther, 1864, *Lycodon ruhstrati* (Fischer, 1886) and *Lycodon subcinctus* Boie, 1827. This arrangement has not changed for the next 75 years. Vogel et al. (2010) reviewed the *Lycodon ruhstrati* complex and described *Lycodon ruhstrati abditus* as a new subspecies from China, and revalidated *Lycodon futsingensis* (Pope, 1928). Detailed examination of banded specimens of the genus led us to the conclusion, that the diversity is much higher in this region and that several species await description.

In the course of our ongoing review of the *Lycodon fasciatus* complex, we came upon two specimens of the genus *Lycodon* from Yunnan, China, which seemed to be different from *L. fasciatus*. A detailed examination showed clear morphological differences which lead us to describe them as new species.

MATERIAL & METHODS

This revision is based on a total of 67 preserved specimens of *Lycodon fasciatus* auctorum examined for their external morphological characters and on several photographed specimens. They are listed in the Appendix I. Comparative material of the *L. ruhstrati* complex is listed under Vogel et al. (2010).

A total of 53 morphological characters were recorded for each specimen. The characters and their abbreviations are listed in Table 1. Not all of these characters have been used for this study, but all of them were compared.

Measurements, except body and tail lengths, were taken with a slide-caliper to the nearest 0.1 mm; all body measurements were made to the nearest millimetre. The number of ventral scales was counted according to Dowling (1951). Half ventrals were not counted except they were present on both sides (divided ventrals). The terminal scute is not included in the number of subcaudals. The dorsal scale row counts are given at one head length behind head, at midbody (i.e., at the level of the ventral plate corresponding to a half of the total number of ventrals), and at one head length before vent. We considered being sublabials those shields that were completely below a supralabial. Values for paired head characters are given in left / right order.

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Table 1. List of morphological characters used in this study and their abbreviation.

N°	Abbreviation	Characters
Morphometry		
1	SVL	Snout-vent length (mm)
2	TaL	Tail length (mm)
3	TL	Total length (mm)
4	Rel TL	Relative tail length TaL/TL
Anatomy		
5	TEETH	Number of upper maxill. teeth (one side)
Scalation		
6	DSR	Dorsal scale rows
7	ASR	Dorsal scale rows at neck
8	MSR	Dorsal scale rows at midbody
9	PSR	Dorsal scale rows before vent
10	Keel	Number of keeled dorsal rows
11	VEN	Ventral plates
12	PreVEN	Number of preventrals
13	VEN not	Ventrals notched or not
14	VEN keel	Ventrals keeled
15	SC	Subcaudal plates
16	ANA	Anal plate: 1: single – 2: divided
17	Lor-l	Number of loreal scale (0 or 1) at left
18	Lor-r	Number of loreal scale (0 or 1) at right
19	Lo touch-l	Loreal scale touches eye at left
20	Lo touch-r	Loreal scale touches eye at right
21	SL-l	Number of supralabials at left
22	SL-r	Number of supralabials at right
23	SL/Eye-l	Numbers of the SL entering orbit at left
24	SL/Eye-r	Numbers of the SL entering orbit at right
25	Larg SL-l	Largest SL left
26	Larg SLrl	Largest SL right
27	IL-l	Number of infralabials at left
28	IL-r	Number of infralabials at right
29	IL-tot	Total number of infralabials
30	IL/1st child	Number of IL in contact with anterior chin shield
31	PreOc-l	Number of preoculars at left
32	PreOc-r	Number of preoculars at right
33	PostOc-l	Number of postoculars at left
34	PostOc-r	Number of postoculars at right
35	ATem-l	Number of anterior temporals at left
36	ATem-r	Number of anterior temporals at right
37	PTem-l	Number of posterior temporals at left
38	PTem-r	Number of posterior temporals at right
39	ParaR	Temporal row containing paraparietals
40	Paras	Plates surrounding paraparietals, see Inger & Marx (1965)
41	Parab	Scales between the paraparietals
Pattern		
42	BODCOL	Body colour1: grey; 2: brown or ochre
43	Bands	Number of bands on body
44	Tail bands	Number of bands on tail
45	Tail venter	Colouration of tail venter
46	Bellycol	Colouration of belly
47	Bellyspeck	Speckling of belly
48	First band	Number of VEN before the first band starts, counted left side
49	Broad base	Number of VEN that are covered at the base of the first band
50	Broad vert	Numbers of vertebral scales that are covered by the first band
51	Edged	Dorsal bands with light margins
52	Coul throat	Colour of the throat
53	Ve throat	Dark VEN on the throat before the first band

The white or light bands on the body and tail were counted on one side. Hardly visible or incomplete bands were counted as one, bands that were fused were counted as two. The collar on the neck was not counted and bands covering the anal shield were added to the bands of the body.

Museum abbreviations

BMNH: The Natural History Museum, London, UK. – BNHS: Bombay Natural History Society, Mumbai, India. – CAS: California Academy of Sciences, San Francisco, USA. – CIB: Chengdu Institute of Biology, Chengdu, People's Republic of China. – FMNH: Field Museum of Natural History, Chicago, USA. – KIZ: Kunming Institute of Zoology, Kunming, People's Republic of China. – MNHN: Muséum national d'Histoire naturelle, Paris, France. – NMW: Naturhistorisches Museum Wien, Austria. – ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. – ZMB: Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany. – ZSM: Zoologische Staatssammlung, München, Germany.

RESULTS

Lycodon synaptor sp. n.

Holotype. BMNH 1905.1.30.63 adult female (tail dissected), from "Tongchuan, Yunnan", today Dongchuan, 100 km north of Kunming, Yunnan Province, People's Republic of China (Figs 1–3). Collected by the J. Graham Expedition, unknown date.

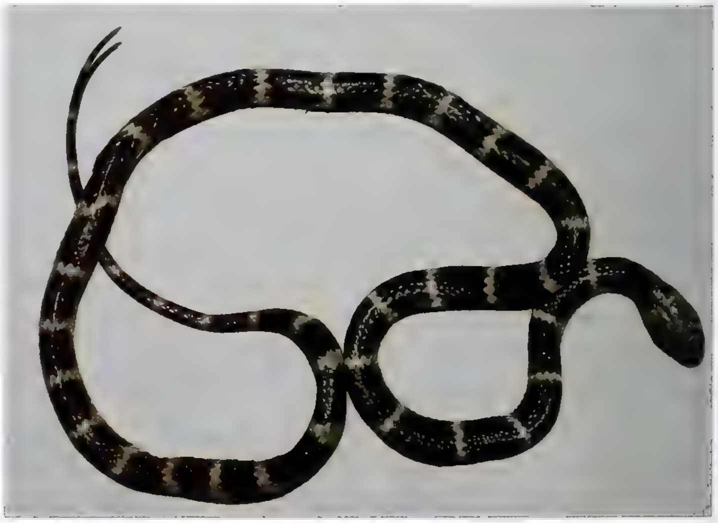

Fig. 1. Dorsal view of preserved holotype of *Lycodon synaptor* sp. n., BMNH 1905.1.30.63 from Dongchuan, 100 km north of Kunming, Yunnan Province, People's Republic of China. Photograph by Gernot Vogel.

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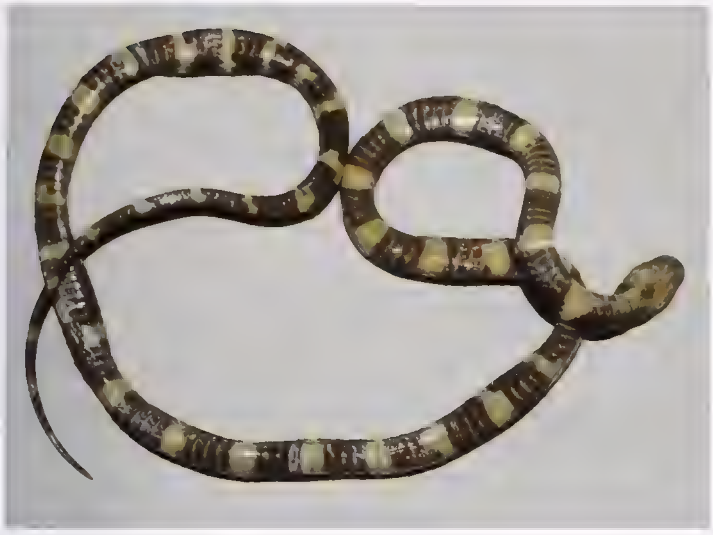

Fig. 2. Ventral view of preserved holotype of *Lycodon synaptor* sp. n., BMNH 1905.1.30.63 from Dongchuan, 100 km north of Kunming, Yunnan Province, People's Republic of China. Photograph by Gernot Vogel.

Paratype. MNHN 1905.0283, adult female (tail dissected), from "Tongchuan Fu, Chine", at present Dongchuan, Yunnan Province, People's Republic of China. Collected by W. F. H. Rosenberg on 21st July 1905.

Diagnosis. A species of the genus *Lycodon* characterized by: (1) loreal scale not entering orbit; (2) 15–17 dorsal scale rows at the forepart of the body and 17 dorsal scale rows at midbody; (3) upper and vertebral dorsal rows (6–7) keeled; (4) 201–203 ventrals in females, males unknown; (5) 68–69 Sc in females, males unknown; (6) a relative tail length of about 0.189–0.192 in females, males unknown; (7) 8 supralabials with SL 4–6 touching the orbit (7) 30–31 narrow white bands on a dark body; (8) width of the first band vertebral 0.5–1.0 scales, on the base 3 ventrals; and (9) the belly with discreet bands throughout.

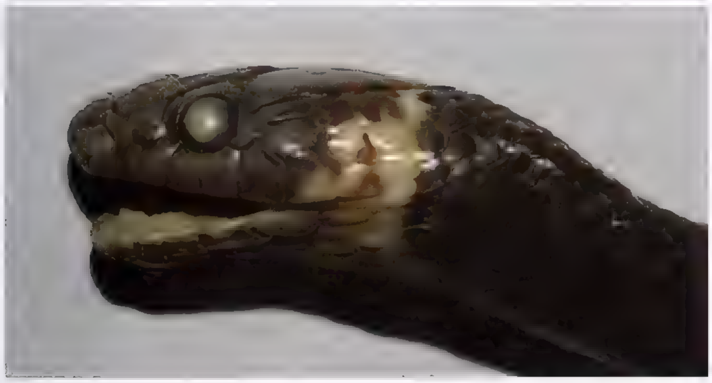

Fig. 3. Lateral view of the right side of the head of preserved holotype of *Lycodon synaptor* sp. n., BMNH 1905.1.30.63 from Dongchuan, 100 km north of Kunming, Yunnan Province, People's Republic of China. Photograph by Gernot Vogel.

The new species can be recognized by the combination of the loreal scale not entering orbit (entering in *L. fasciatus* sensu stricto), its narrow dorsal bands, with the first band starting at ventral 5–9 (more irregular in *L. fasciatus* [Fig. 4] and species of the *L. ruhstrati* group, where they usually start later) and the dark throat, which usually is light in other species of the *L. fasciatus* group and the *L. ruhstrati* group. Most other characters match with *Lycodon fasciatus*.

Detailed comparisons with other species of the genus *Lycodon* appear below in the Discussion.

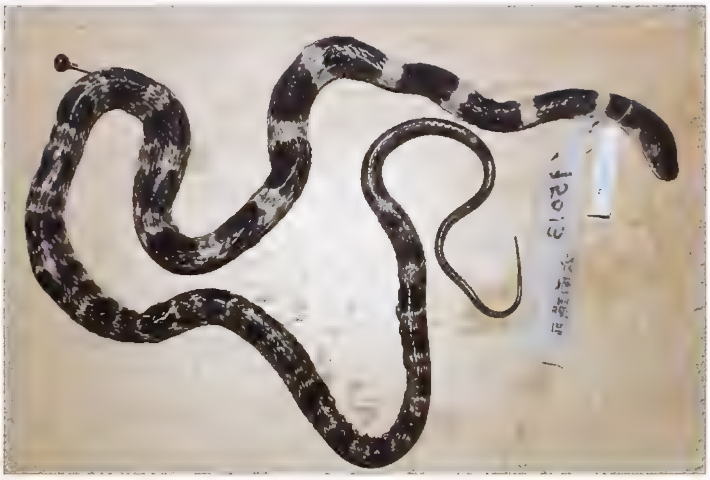

Fig. 4. Dorsal view of *Lycodon fasciatus*. CIB 9804, from Ruili City, Yunnan. Note the irregular bands. Photograph by Gernot Vogel.

Etymology. This species is indirectly named in honour of Dr. Wolfgang Böhme. It was always a publicized aim of Wolfgang Böhme to unite professional and amateur herpetologists. We, both authors have always been amateur herpetologists, so it is a delight for us to dignify his efforts towards this aim. The specific name *synaptor*, a noun in apposition, stems from the Greek word "συναψις" meaning "a connection". In this case, this noun underlines the connection of these two kinds of herpetologists.

We suggest the following common names: *Boehme's wolf Snake* (English), *Böhmes Wolfszahnnatter* (German).

Description of the holotype. *Habitus*. Body elongate, somewhat laterally compressed; head flattened anteriorly, well distinct from the neck; snout depressed and elongate; nostril oval, large, in the middle of the nasal. Eye moderate, with a vertically elliptic pupil.

SVL 374 mm; TaL 89 mm; TL 463 mm.

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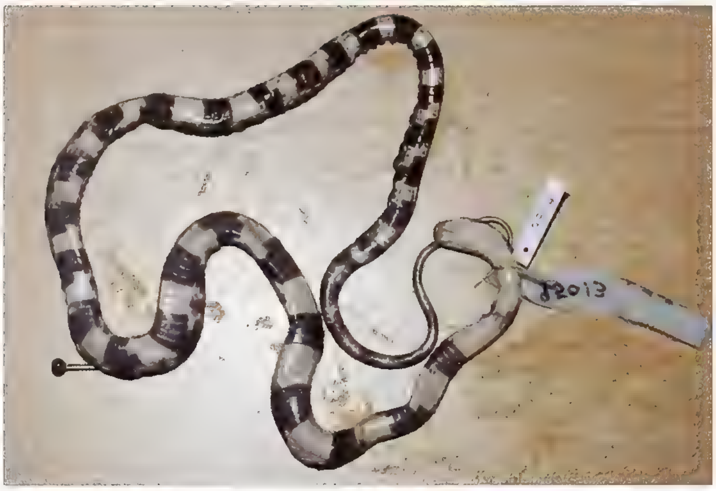

Fig. 5. Ventral view of *Lycodon fasciatus*. CIB 9804, from Ruili City, Yunnan. Note he whitish colouration of the anterior part and te speckling of the posterior part. Photograph by Gernot Vogel.

Dentition. A total of 10 maxillary teeth, with the following formula: 4 small anterior teeth + 2 strongly enlarged teeth + a wide gap + 2 small teeth + a small gap + 2 strongly enlarged, posterior teeth.

Body scalation. 201 VEN (+ 2 preventrals), 68 SC, all paired. Anal single. Dorsal scales in 17–17–15 rows, the 7 upper rows feebly keeled. Vertebral row not enlarged. No apical pit detected.

Head scalation. Rostral, triangular, hardly visible from above; nasal vertically divided by a furrow below and above the nostril; two small, trapezoidal internasals, widely in contact each with the other and with prefrontals; two large prefrontals, longer and wider than internasals; a rather small ogive-shaped frontal, about 1.3 times longer than wide and about 0.8 time as long as the suture between the parietals; 2 large parietals, each edged with three large scales, 2 upper temporals and a larger paraparietal posteriorly; 1 / 1 wide, triangular supraocular; 1 / 1 small preocular, located above the posterior part of loreal; 2 / 2 postoculars, about the same size; 1 / 1 subrectangular loreal, elongateand narrow, not entering orbit, in contact with SL 2 and 3, the large preocular, the prefrontal (long contact) and the posterior part of nasal; 8 / 8 SL, of which the first four are higher than long, SL 1–2 in contact with nasal, SL 3–5 entering orbit, 6th and 7th SL largest; 2+2 / 2+2 temporals, lower anterior temporal a bit broader than upper one, posterior temporals smaller; 8 / 8 infralabials, IL 1–4 in contact with the first pair of sublinguals; anterior and posterior pair of sublinguals of about same length, but anterior pair wider.

Coloration in preservation. Body and tail dark blackish-brown, with 31 crossbands on body and 9 on tail, narrow and cream, not speckled; these crossbands, about 1 dorsal scale long, widen at their ventrolateral limit, up to about 5–7 dorsal scale long; the first crossband, beginning at the level of VEN 9; the second crossband is 8 scale rows behind the first one; 9 cream crossbands on the tail, also not speckled.

The head is uniformly blackish-brown, a broad nuchal collar extends from the 6th and 7th supralabial across the lower posterior temporal across the posterior half of the parientals. The underside of the head ist dark in the anterior half and cream in the posterior one; the throat is cream, with a dark clowdy spot on the preventrals and the first ventral.

The venter is dark, with faint cream bands rather regular, 2 ventrals wide and with 3–4 ventrals in between. Within these bands some ventrals are dark on one half and cream on the other, especially in the posterior part of the body. The under surface of the tail is banded as the venter with the cream bands about 1.5 SC wide.

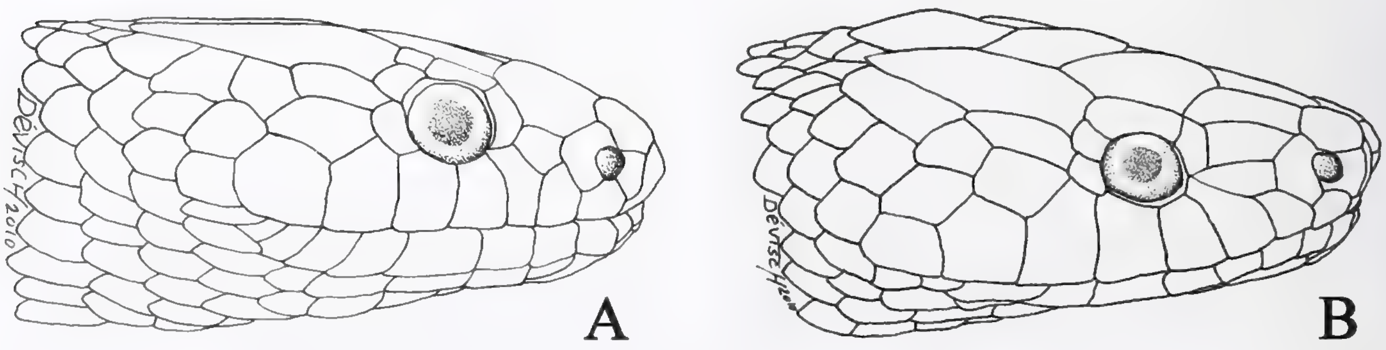

Fig. 6. Comparison of lateral head scalation of *Lycodon synaptor* sp. n. (BM 1905.1.30.63 Holotype) and one *L. fasciatus* (BNHS 1223) where the Lo touches the eye. This is the case only in 6.3% of all cases seen by us. Please note that in *L. synaptor* sp. n. the Lo is well separate from the eye by the preocular scale, whereas it is tapering and narrow in the *L. fasciatus*, where it is more or less inserted between 2 sales and falls short from the eye. Drawings by Dick Visser.

Table 2. Pholidosis of the two type type specimens of *Lycodon synaptor* sp. n.

Characters	BMNH 1905.1.30.63 holotype	MNHN 1905.0283 paratype
Sex	Female	Female
SVL	374	395
TaL	87	92
Rel TL	0.192	0.189
ASR	17	15
MSR	17	17
VEN	201	203
SC	68	69
Lo enters eye	no	no
Dorsal bands	31	30
Tail bands	9	9
First band at VEN no	9	5
Broad base [VEN]	7	3
Broad vertebral [Dorsals]	2	1

Variation. The paratype, MNHN 1905.0283, agrees in most respects with the description of the holotype with the throat being dark instead of light. The maxilla are missing in the paratype. A comparison of the most important morphological characters is summarized in Table 2.

Distribution. China. *Lycodon synaptor* sp. n. is currently only known from the region of Dongchuan, Dongchuan County, in the province of Yunnan, China.

Biology. There is no information available on the biology of this species. However, the region of Dongchuan is highly mountainous. Dongchuan is located between high mountains of the ranges known as Gongwang Shan and Liangwang Shan. In the area, the highest point is 4.344 meters high, and lowest is 695 meters asl.

DISCUSSION

Lycodon synaptor sp. n. is superficially similar to *L. fasciatus* but differs from the whole *L. fasciatus* group (including *L. butleri*) by the loreal, which does not enter orbit in *L. synaptor*. We have examined six specimens (out of 35) of *Lycodon fasciatus* sensu stricto in which the loreal does not enter orbit (eight occurrence, three times on both sides [4.7 %]), but the morphology of the anterior region of the eye is different. In specimens of *L. fasciatus* in which the loreal does not enter orbit, the posterior region of this narrow scale is very tapering (Fig. 6). Its apex is more or less inserted between the preocular and the 4th SL and falls short from the eye. In contrast, in *L. synaptor*, the loreal scale is well separated from the orbit by a broad preocular. The tail is a bit shorter in *L. synaptor* sp. n. (0.189–0.192 vs. 0.190–0.219 in 29 females of *L. fasciatus*). There are also differences in the shape of the bands and the colouration of the belly (compare Figs 2 and 5). *L. synaptor* sp. n. has eight infralabials, whereas only one specimen out of 60 specimens of *L. fasciatus* had eight infralabials on both sides and rarely that character is seen on one side (5 %) in *L. fasciatus*. *L. synaptor* sp. n. has less subcaudals than *L. fasciatus* (68–69, x = 68.5, versus 70–88, x = 79.9 with one outlier having 67 subcaudals). For a complete comparison of scale counts see Table 3.

L. synaptor sp. n. differs from the other Chinese and Indochinese species as follows: from *L. subcinctus* by the fact that in *L. synaptor* sp. n. both a loreal and a preocular are present. From *L. laoensis, L. zawi* and *L. capucinus* it differs by the anal shield which is single in *L. synaptor* sp. n. but divided in the latter two species. Furthermore the colouration is much different. From the *L. ruhstrati* group it differs by the colouration of the bands (small, regular, completely light in *L. synaptor* sp. n., getting broader posteriorly, irregular and partly speckled with brown in the *L. ruhstrati* complex), by the number of infralabials (eight in *L. synaptor*, nine to ten in the *L. ruhstrati* group) and by the colour of the belly, which is speckled or uniform light in the *L. ruhstrati* group, but clearly banded in *L. synaptor* sp. n. From *L. paucifasciatus* Rendahl, 1943, occurring in Vietnam, *L. synaptor* sp. n. differs by the number of anterior dorsal scale rows (15–17 in *L. synaptor* sp. n. and 19 in *L. paucifasciatus*).

Table 2. Important characters in the *Lycodon fasciatus* / *ruhstrati* groups.

Lycodon	*fasciatus*	*synaptor* sp. n.	*ruhstrati*	*futsingensis*	*cardamomensis*
n females	35	2	23	6	1
TL, females	N=29 679	N=2 487	N=22 876	N=5 773	N=1 545
Rel TL, females	0.190–0.219 N=29	0.189–0.192 N=2	0.207–0237 N=22	0.205–0.217 N=11	0.25 N=1
VEN, females	180–219 N=35	201–203 N=2	217–229 N=23	198–208 N=13	223 N=1
SC, females	(67) 70–88 N=29	68–69 N=2	90–108 N=21	78–85 N=5	92 N=1
IL both sexes	9–10 (8)[*] N=120	8 N=2	10 (9.11) N=86	9–10 (11) N=44	10 N=4
Bands	19–43 N=60	30–31 N=2	19–46 N=45	19–33 N=22	12–13 N=4
Tail bands	7–21 N=62	9 N=2	10–23 N=43	9–18 N=21	6 N=4
First band	5–18 N=51	5–9 N=2	8–17 N=34	13–23 N=18	unknown
Broad base	3–12 N=51	3 N=2	5–9 (12) N=34	5–8.5 N=18	unknown
Lo enters orbit	Yes (rarely not[**]) N=126	No N=4	No (rarely yes[***]) N=86	No N=44	No N=4
Belly banded	Yes N=63	Yes N=2	No N=25[****]	No N=22	No N=4

[*] 8 in 6 cases (5 %), in one specimen from Shillong on both sides (1.6 %)

[**] not entering in 8 occurrences (6.3 %), three times on both sides (4.7 %) (see above)

[***] in 6 specimens, all from Fujian the Lo touched the eye.

[****] banded in juveniles only

Werner (1922) described *Dinodon yunnanensis* from Yunnanfu, now Kunming, Yunnan Province. This species was synonymised with *Lycodon fasciatus* by Pope (1935: 188), but according to our unpublished data, this taxon might be valid. In any way this name is available, so we compared *Lycodon synaptor* sp. n. with *Dinodon yunnanensis* Werner, 1922 for which we re-examined the holotype (NMW 23417; adult female). *Lycodon synaptor* sp. n. differs from *D. yunnanensis* mainly by the loreal which is touching the eye in *D. yunnanensis*, but also by the number of ventrals (201–203 against 193) and the number of bands on the body (30–31 vs. 23) and the number of infralabials (eight vs. nine in *D. yunnanensis*).

While preparing a review for the *Lycodon fasciatus* group, we found quite a lot of obviously independent lineages,

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which seem to constitute distinct species. Some of them are restricted to small areas. A discussion of these lineages will follow in the main review (Vogel & David in prep.). *Lycodon synaptor* sp. n. differs so much from other members of the group that we decided to describe it separately. The closest localities we got from *Lycodon fasciatus* are from the vicinity of Kunming in Yunnan province, which lies about 100 km south of Dongchuan. This latter place (previously Tongchuan or Tongchuan Fu) is the type locality for several reptile species, as *Cuora yunnanensis* (Boulenger 1906), *Nanorana yunnanensis* (Anderson, 1879), *Odorrana grahami* (Boulenger 1917) and *Bombina maxima* (Boulenger 1905). It is a relatively small city that had about 300.000 inhabitants in 2006.

Revised Key for the genus *Lycodon* in China

According to our data, there are several unnamed species of the genus *Lycodon* living in China. So this should be regarded as preliminary key.

1. Both a loreal and a preocular scales present **2**
Either loreal or preocular absent .... *L. subcinctus*
2. Anal divided **3**
Anal single **4**
3. Anterior chinshields not more than 1.5 times longer than posterior ones; loreal in extensive contact with internasal, when adult no crossbands on body .... *L. capucinus*
Anterior chinshields 2 to 3 times longer than posterior ones; loreal not, or barely in contact with internasal (very rarely a strong contact), when adult yellow crossbands on forepart of body .... *L. laoensis*
4. Belly banded **5**
Belly not banded **6**
5. Lo not touching the eye, 8 lower labials .. *L. synaptor* sp. n.
Lo usually touching the eye, usually 9–10 lower labials .... *L. fasciatus*
6. Dorsal rows keeled .... *L. ruhstrati abditus*
Dorsal rows smooth .... *L. futsingensis*

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APPENDIX I

Additional comparative material of *Lycodon fasciatus*

India. Shillong, Assam, BMNH 92.1.25.1; BMNH 1908.6.23.6; BMNH 1908.6.23.8; BMNH 1907.12.16.28–29; BMNH 94.10.4.2; BNHS 1219–20, 1229.

Laos. Xieng-Khouang, Laos, MNHN 1928.69.

Myanmar. Maymyo, Burma, BMNH 1925.12.22.15–16; Mogok, Burma, BMNH 1900.9.20.5–7; BMNH 1901.4.26.1Mogkok, Burma, BNHS 1221 "Burma", BMNH 1908.6.23.9–11 ; Burma, BNHS 1218; Toungyi, Shan State, Myanmar, BMNH 91.11.26.31; Bhamo, Burma, BMNH 1925.4.2.28; Kachin Hills, Burma, BMNH 1925.9.17.10–11; South Shan State, BMNH 1908.6.23.14; Burma-Siam Border, BMNH 1937.2.1.12; Rangoon, Burma, BMNH 1940.3.3.3; Maymyo, Burma, BNHS 1222–24; Thandung Hills, BNHS 1228.

People's Republic of China. Western China CAS 55147; Yunnan, MNHN 1919.148; "Yunnan Fu" (holotype of *Dinodon yunnanensis*), NMW 23417; Kuantun, ZSM 75/1938; Kunming, Yunnan, BMNH 1930.11.16.4; Ruili City, Yunnan, CIB 9804; RuiLi, Yunnan,, CIB 9805; XiShuangBanNa, Yunnan, CIB 9806, CIB 9808, CIB 9809; LongChuan GongWa, Yunnan, KIZ 74 I 0035; LongChuan HuSa, Yunnan, KIZ 74 I 0145; Tengchong County, Yunnan KIZ 74 II 0262; Menglian, Yunnan, KIZ 75 I 473; TengChong TuanTian, Yunnan, KIZ 74 II 0263; Kunming, Yunnan, KIZ 73009; Kunming, Yunnan, KIZ 77004; Kunming city, Yunnan, KIZ 83007; Yunnan, KIZ 83017; FMNH 15148; Tibet; MNHN 1921.0465 Tibet; Yunnan,; ZMB 65453

Thailand. Chiang Mai, Thailand, FMNH 178369; CAS 172715, Southern Thailand ? FMNH 178368, Nan province Thailand FMNH 270716.

Vietnam. Phong Nha, Vietnam, ZFMK 86448–50 (GenBank: EU999214-215); ZFMK 80665; Ziegler unreg.

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A crowned devil: new species of *Cerastes* Laurenti, 1768 (Ophidia, Viperidae) from Tunisia, with two nomenclatural comments

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Abstract. A distinctive new species of the viperid genus *Cerastes* is described form Tunisia. It is closely related to *Cerastes vipera* but easily distinguishable from this invariably hornless species by having tufts of erected supraocular scales forming little crowns above the eyes. These crown-like tufts consist of several vertically erect, blunt scales which differ drastically from the supraocular horns of *C. cerastes* or *C. gasperettii* that consist of one long, pointed scale only. Although the new species is based on only one single specimen, further specimens had originally been available but were subsequently lost in private terraria.

The taxonomic status of the nomen *"Cerastes cerastes karlhartli"* is discussed and the name is found to be unavailable (nomen nudum). Also the authorship of "*Cerastes cornutus*" is discussed and ascribed to Boulenger.

Key words. *Cerastes cerastes*, *Cerastes vipera*, *Cerastes* sp. n., *Cerastes c. karlhartli*, *Cerastes cornutus*, horned viper, North Africa, Tunisia.

INTRODUCTION

The genus *Cerastes* Laurenti, 1768 includes only five taxa (three species and two subspecies), which are distributed in northern Africa and on the Arabian Peninsula. All species are stout-bodied and, as desert snakes, are characterized by many xeromorphic physiological and morphological adaptations. The most impressive adaptations are the strongly keeled serrated lateral body scales, a character they share with their proposed sister taxon *Echis* (Joger & Courage 1999, Pook et al. 2009), but not with the also sand living snakes of the genus *Bitis*.

The largest member of the genus is *Cerastes cerastes* (Linnaeus, 1758) with a maximum body size of 80 cm and an average size of 35 to 60 cm. The distribution range of the nominotypic form includes all Saharan countries with a southernmost distribution in Sudan (Phelps 2010) and the northernmost in central Tunisia (Schleich et al. 1996). Eastwards it reaches the Sinai, Israel and Jordan (Phelps 2010). *Cerastes c. cerastes* occurs in sandy and rocky deserts and around well vegetated oases but not in windblown dunes (Phelps 2010). *Cerastes c. hoofienii* Werner & Sivan 1999, the second subspecies occurs in the extreme southwestern edge of the Arabian Peninsula in Yemen and Saudi Arabia.

The second North African species is *C. vipera* (Linnaeus, 1758). Its distribution range is very similar to *C. cerastes* but more restricted to the Saharan Desert and reaches eastward to the Sinai and Israel as it only occurs in dune systems. Therefore, according to Phelps (2010) both species were never recognized as locally syntopic, but Joger (2003) found both species occurring parapatrically at the edge of the Grand Erg Oriental in Tunisia. *Cerastes vipera* is the smallest viper of the genus and grows up to a maximum size of under 50 cm with an average about 35 cm.

The remaining species is *Cerastes gasperettii* Leviton & Anderson, 1967 with its subspecies *gasperettii* and *C. g. mendelssohni* Werner & Sivan, 1999. It is distributed on the Arabian Peninsula and eastwards to Iraq and Iran, overlapping with other *Cerastes* species in its distribution only in the southern Sinai and the northwestern edge of the Arabian Peninsula.

The common name 'Horned Vipers' is misleading as not all species and not all populations possess supraocular horns. In *C. cerastes* and *C. g. gasperettii* specimens usually bear horns but several populations are hornless. If present, the horns are formed by a long, sulcated, single

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spike above each eye, usually surrounded by a ring of elongate spinose but non-sulcated scales. This polymorphism is also known in other viperid snakes as the supraocular horns of *Bitis caudalis* and the supranasal horns of *Bitis gabonica* are absent in some specimens (FitzSimons 1962, Branch 1988). However, *C. g. mendelssohni* and *C. vipera* are strictly hornless as opposed to the other taxa.

Gasperetti (1988) described the characters of the genus *Cerastes* as (a) the eyes are small to moderate and separated from the labial scales by several rows of small scales; (b) body scales with club or anchor shaped keels, not extending to the extremity of the scales; (c) lateral body scales smaller than vertebral scales; (d) anal scale entire; and (e) ventral scales with an obtuse keel on each side. For many decades, only two species, *C. cerastes* and *C. vipera*, were recognized but Werner (1987) and Werner et al. (1991) elevated *C. gasperettii* to full species status, which was later accepted by many authors (e.g. Schätti & Gasperetti 1994, Phelps 2010).

Following Baha el Din (2006) the two African species are easy to distinguish. In *C. vipera*, supraocular horns are never present, there are less than 14 interorbitals and counts of ventral scales are below 120, whereas in *C. cerastes* there are more than 14 interorbitals and more than 130 ventrals. Schleich et al. (1996) distinguished the two snakes mainly by the position of the eye (lateral in *cerastes* and directed upwards in *vipera*), by the presence or absence of a supraocular horn and by the number of interorbital scales (15–21 in *cerastes* and 9–13 in *vipera*). Geniez et al. (2004) distinguished both species by their longitudinal rows of dorsal scales at midbody (27–35 in *cerastes*; 23–27 in *vipera*), but also mentioned the eyes on the top of the head in *C. vipera*.

In the collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) a specimen of *Cerastes* is present, which is generally similar to *C. vipera* but clearly distinct in possessing supraocular crown-like scale tufts instead of horns of a solitary scale. Because of this striking character, as such tufts or horns are absent in *C. vipera*, the specimen was examined and compared with other *Cerastes* specimens of the ZFMK collection and with relevant literature.

MATERIAL & METHODS

This description is based on the comparison of 75 preserved *Cerastes* specimens and three vouchers of other snakes of the ZFMK collection (see below) and the relevant literature (Jooris & Fourmy 1996; Schleich et al. 1996; Geniez et al. 2004; Baha el Din 2006; Phelps 2010). Measurements were taken with a digital-calliper to the nearest 0.1 mm. The number of ventral scales was counted excluding the anal scale. The number of subcaudals included the terminal scale. The dorsal scale row count is given as (a) fore body: one head length behind head, (b) midbody at the level of the ventral plate corresponding to a half of the total number of ventrals), and (c) hind body one head length before vent.

For SEM images a Hitachi S-2460N was used to compare the scale morphology of different snake species. Dorsal body scales from about the middle of the dorsum were used from the following specimens: *Cerastes* sp. n. (ZFMK 58054, Tunisia), *Bitis peringueyi* (Boulenger, 1888) (ZFMK 44887: Namibia, Swakopmund) and *Bitis schneideri* (Boettger, 1886) (ZFMK 88450: Namibia, without locality). These were compared with SEM-photographs from *C. cerastes* and *C. vipera* published by Joger & Courage (1999).

Material examined. *Cerastes cerastes*: **ALGERIA**: ZFMK 7649-7650, Colomb-Béchar; ZFMK 18082, 60km west of Tougourt; ZFMK 18083-084, 20km north of Bou-Saada; ZFMK 18085, Hoggar Mts., Guelta Afiale; ZFMK 23000, south of Temassinin, Flatters; ZFMK 23001, Bordj-Saada; ZFMK 23002-005, south of Ouargla; ZFMK 38248, 20km south of Djanet. **EGYPT**: ZFMK 22996, Isna (=Esne); ZFMK 22997, vicinities of Cairo; ZFMK 50295, Aswan desert; ZFMK 50296, Faijum desert; ZFMK 50299-300, Nada el Wahda desert; ZFMK 32488, 50297-298, without locality. **LIBYA**: ZFMK 63668, Wadi Matendus; **Mauretania**: ZFMK 17593, Chami. **MOROCCO**: ZFMK 65218, Draa Valley. **NIGER**: ZFMK 20258, between Arlit and Agadez, 120km south of Arlit; ZFMK 36629, 40km northeast of Wadi Gougaram. **SUDAN**: ZFMK 32462, 100km southwest of Burget Tuyur depression; ZFMK 32463, Dafur, Teiga Mts., west of Eisa; ZFMK 32464, Darfur, Djebel Rahib; ZFMK 33697, Nubian desert, 130km southeast of Wadi Halfa; ZFMK 33698-700, Wadi Halfa; ZFMK 38410, 80km north of Port Sudan. **TUNISIA**: ZFMK 18081, 10km west of Tozeur, Oasis Stil; ZFMK 22998-999, Tunisian desert; ZFMK 29047, El Hamma du Djerid near Tozeur; ZFMK 29809-812, 29046, Tozeur; ZFMK 47020-024, between Tozeur and Nefta; ZFMK 49858, Oasis Nefta. ***Cerastes gasperettii*:** **IRAQ**: ZFMK 18843-844, vicinities of Basrah; ZFMK 19414, Basrah. **KINGDOM OF JORDAN**: ZFMK 44340, Wadi Araba, Fidan. **KINGDOM OF SAUDI ARABIA**: ZFMK 43659, 100km northeast of Riyadh. **UNITED ARAB EMIRATES**: ZFMK 52419, Al-Mundam. ***Cerastes vipera*:** **ALGERIA**: ZFMK 22984, El Alia; ZFMK 41176, Ain Sefra. **EGYPT**: ZFMK 22989-994, 50339, vicinities of Cairo; ZFMK 22995, Sinai, Wadi Arish; ZFMK 50301-302, El Wasta, Abwid desert. **LIBYA**: ZFMK 32489, Tripolis. **MAURETANIA**: ZFMK 17594, Chami. **TUNISIA**: ZFMK 22985-988, Tunesian Sahara, without locality. **WESTERN SAHARA**: ZFMK 83340, Laayoune Plage; ***Bitis caudalis*:** **NAMIBIA**: ZFMK 65212, Swakopmund; ***Bitis peringueyi*:** **NAMIBIA**: ZFMK 88453, without locality. ***Bitis schneideri*:** **NAMIBIA**: ZFMK 88450, without locality.

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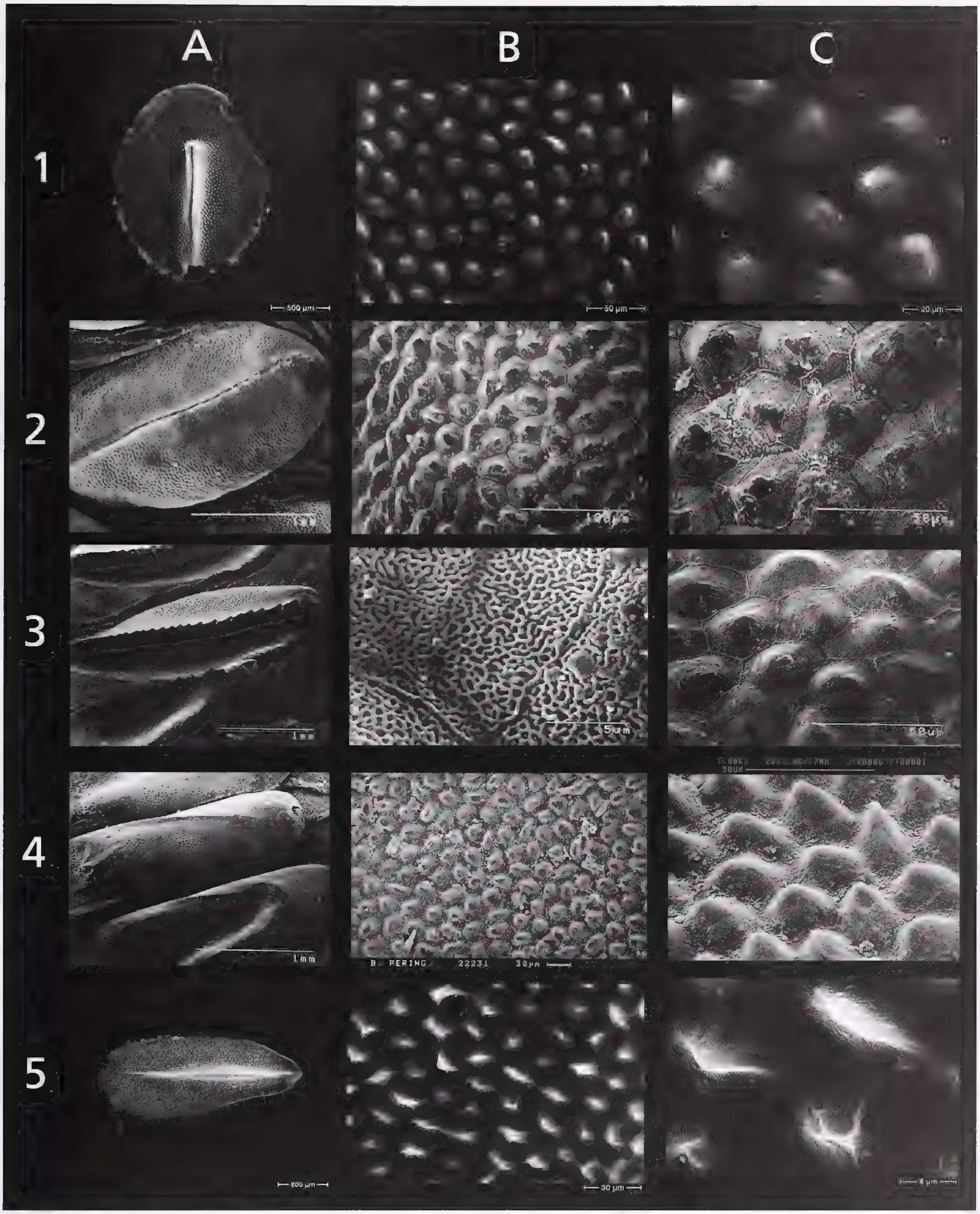

Fig. 1. SEM images of dorsal body scales of viperid snakes.
1= *Cerastes* sp. n. from central Tunisia (ZFMK 58054); **2**= *Cerastes cerastes* published by Joger & Courage 1999; **3**= *Cerastes vipera* published by Joger & Courage 1999; **4**= *Bitis peringueyi*, 4A published by Joger & Courage 1999, 4B & 4C from Namibia (ZFMK 44887), and 4A= published by Joger & Courage 1999; **5**= *Bitis schneideri* from Namibia (ZFMK 88450).
A= dorsal scale, complete; **1B**= dorsal scale, verrucate, secondary structure; **2B**= dorsal scale, verrucate, secondary structure; **3B**= dorsal scale, liniar, tertiary structure; **4B**= dorsal scale, verrucate to cristate, secondary structure; **5B**= dorsal scale, cristate, secondary structure; **1C**= dorsal scale, secondary structure in detail; **2C**= dorsal scale, secondary structure in detail; **3C**= dorsal scale, secondary structure in detail; **4C**= dorsal scale, secondary structure in detail; **5C**= dorsal scale, secondary structure in detail.

RESULTS & DESCRIPTION

The comparison of the fine structure of a dorsal, non-rattling scale of the single specimen with images of lateral, rattling scales of *Cerastes* and lateral scales of *Bitis* (see fig. 1) shows similarities between the single specimen and *Cerastes*. On the other hand, differences of the typical scale fine structure of *Bitis* are distinct enough to recognize the single specimen as a non-*Bitis* species. The structure typical in *Bitis* specimens is obvious in *Bitis schneideri* (fig. 1.5). They possess a structure of slender, elongated bulges, which are very distinct from *Cerastes*. However, *Bitis peringueyi*, (fig. 1.4) also a sand burrowing snake, is the only species of *Bitis* showing a similar scale structure to *Cerastes* species, but obvious from figure 2, this species is very distinct from the new species of *Cerastes*.

However, all *Cerastes* species are similar in their verrucate secondary structure; cell borders are well visible. These borders are invisible in the cristate or verrucate secondary structure of *Bitis* species.

The comparison of the voucher with *C. vipera* and *C. cerastes* results in a morphological similarity to *C. vipera*. Both are similar in body size, shape of the nostril and head scalation (see fig. 2, tab. 1). However, in other aspects they are clearly distinct: the specimen has lower scale counts as in *C. vipera* in its morphological variation of the entire distribution in northern Africa. The specimen possesses supraocular horns, which are absent in *C. vipera* and horns, encompassing several scales, are also not known in *C. cerastes*. Therefore, we regard this specimen as a new species of *Cerastes*:

Cerastes boehmei sp. n.

Holotype. ZFMK 58054. Female specimen from Tunisia, SW Remada, east of Djebel National Park, close to the road midway between Beni Kadeche (Bani Kheddache) and Ksar el Hallouf, leg. T. Holtmann, 1991.

Diagnosis. This new species of *Cerastes* is characterized by: (a) head depressed, eyes on the lateral part of the head but slightly directed upwards; (b) supraocular coronets (crowns) present, consist of several sulcated, medium sized scales, instead of the supraocular horn formed by a single sulcated long scale in *C. cerastes* or *C. gasperettii*; (c) nostril slit-shaped; (d) low number of interorbital scales; (e) 19–26–16 dorsal scale rows around fore-, mid- and hind body.

Differential diagnosis. The new species differs from (a) *C. vipera* in possessing supraocular coronets, a low number of interocular scales (7 instead of 9–13 fide Schleich et al. [1996], but 6–13 fide Jooris & Fourmy [1996]), a lower number of circumocular scales (11 instead of 19–29 fide Jooris & Fourmy (1996), a lower number of supralabial/infralabial scales (11–12/12–11 instead of 20–33/19–27 fide Jooris & Fourmy [1996]) and a lower number of subcaudal scales (25 instead of 33–57 fide Jooris & Fourmy [1996]). Counts of dorsal scale rows around midbody are ambiguous and depending on the method of counting (see fig. 3). They differ from *C. vipera* (21 instead of 23–27 fide Phelps [2010]) or lie with 26 scale rows within this range; from (b) *C. cerastes* in a lower number of interocular scales (7 instead of 15–21, fide Schleich et al. [1996]), in its smaller size, in possessing a slit-shaped nostril, in possessing supraocular coronets each formed by more than one elongated scale; and finally from (c) *C. gasperettii* in possessing supraocular coronets each formed by more than one elongate scale and in possessing a slit-shaped nostril.

From all recognized synonyms of *C. vipera* (mainly *C. vipera inornatus* Werner, 1929 and *C. richiei* Gray, 1842) the new species differs in possessing supraocular coronets, whereas the synonymised taxa are lacking horns or equivalent structures.

From the recognized synonyms of *C. cerastes* (mainly *C. c. mutila* Doumergue, 1901) the new species differs in possessing supraocular coronets, as all synonymised taxa are lacking horns or equal structures. Following Boulenger (1896) *Cerastes cornutus* Boulenger, 1896 (see also nomenclatural comment as part of the discussion), regarded as a synonym of *C. cerastes* following e.g. Schleich et al. 1996, is also with either horn-bearing or hornless individuals, but differs from *C. boehmei* sp. n. in a higher number of interorbital scales (15 to 21), in possessing supraocular horns made up of a single scale, a higher number of scale rows around midbody (27–35) and a higher number of ventral (130–165) scales.

Description of holotype (fig. 4). *Habitus*. Body elongate and slender, somewhat compressed and oval in profile; head flattened, triangular and well distinct from neck; Eye small to moderate, with vertically elliptical pupil, on upper lateral side, but nearly on top of head; nostril slit-shaped, slightly longer than first supralabial scale.

Measurements (in mm): Total length: 218.5; head length: 16; head width: 9.4; head height: 5.5; snout-vent length: 195; tail length: 25.5.

Scalation of head: Rostral broader than high, semicircular, slightly visible from above; menthal scale only in contact and smaller than first infralabial scale, followed by two large chinshields; nasal scale divided by large scale

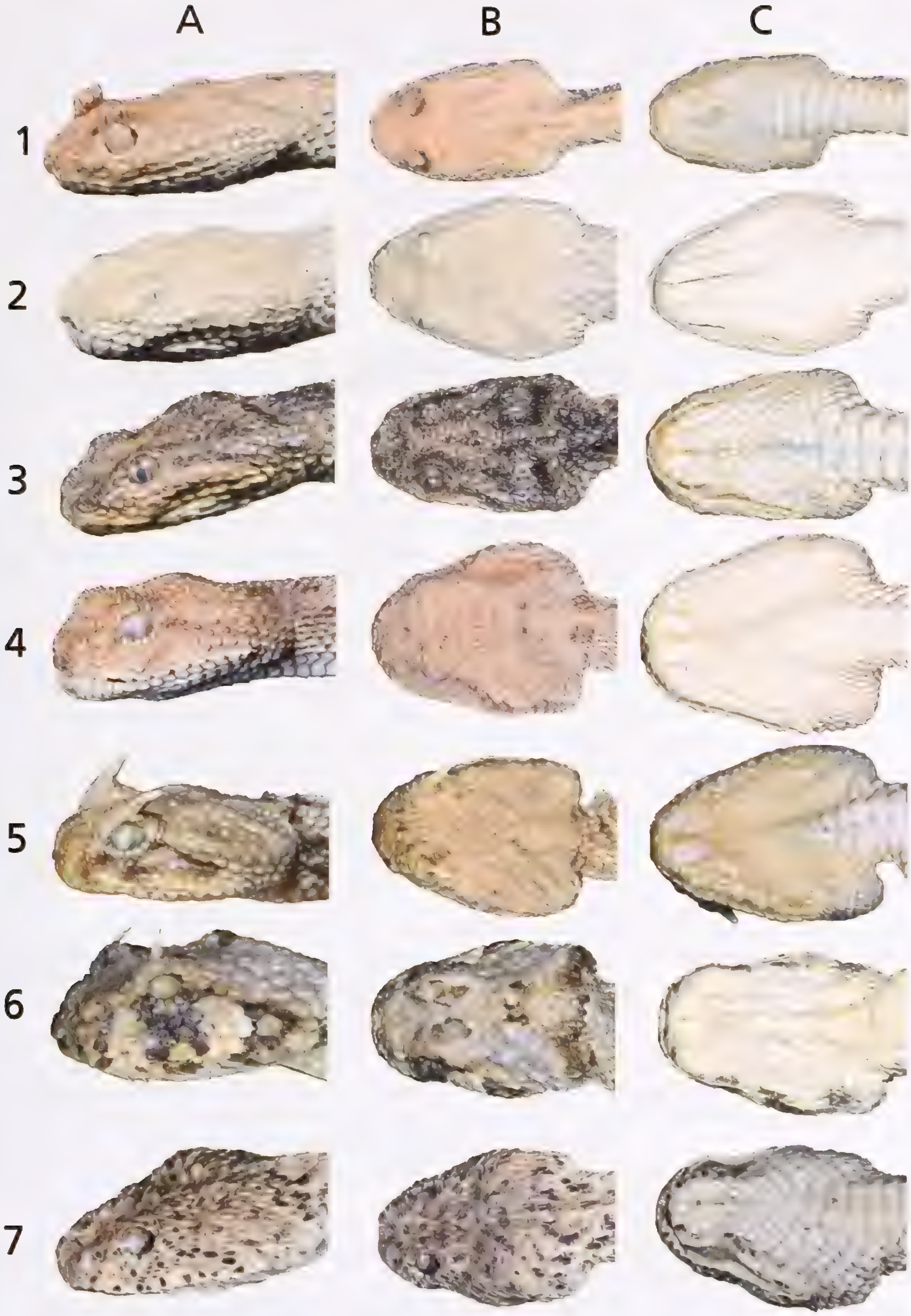

Fig. 2. Comparison of different viperid snakes from Africa.
1= *Cerastes boehmei* sp. n.: ZFMK 58054, Tunisia; **2=** *Cerastes vipera*: ZFMK 22985, Tunisia, without locality; **3=** *Cerastes vipera*: ZFMK 83340, Western Sahara, Laayoune Plage; **4=** *Cerastes cerastes*: ZFMK 63668: Libya, Wadi Matendus; **5=** *Cerastes cerastes*: ZFMK 65218, Morocco, Draa Valley; **6=** *Bitis caudalis*: ZFMK 65212: Namibia, Swakopmund; **7=** *Bitis peringueyi*: ZFMK 88453: Namibia, without locality. **A=** head in profile; **B=** head from above; **C=** head from below.

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Table 1. Comparison of the three *Cerastes* species occurring in northern Africa.

	C. boehmei sp. n.	*C. vipera**	*C. cerastes***
Interorbital scales	7	less than 14 (6–13)	more than 14 (14–21)
Ventral scales	110	below 120	more than 130
Subcaudal scales	25	33–57	18–42
Position of the eye	lateral	directed upwards	lateral
Supraocular horn	present	absent	present/absent
Scale rows around midbody	21 (26)***	23–37	27–35
Circumocular scales	11	19–29	–

*=fide Jooris & Fourmy 1996, Schleich et al. 1996, Baha el Din 2006, Phelps 2010. **= fide Schleich et al. 1996, Baha el Din 2006, Phelps 2010. ***= see fig. 3

bearing nostril at its upper fringe, with smaller overlaying scale; five, more or less trapezoidal internasal scales, the two outer scales twice as large as three inner scales, all keeled; no enlarged prefrontal scales; occipital tubercle absent; supraocular coronets present, consist of elongate, sulcate scales, four on left, five on right side; 11 circumocular scales on each side; interorbital scales 7 at midlevel of supraocular coronets; loreals 3 on each side; supralabial scales: 11 on left, 12 on right side, only first in contact with nasal scale, three scales between supralabial scales and eye (including ocular scale); infralabial scales: 12 on left, 11 on right side.

Scalation of body: Ventral scales: 110; subcaudal scales: 25; number of scale rows around fore-body: 19, mid-body: 21 or 26 (see fig. 3), hind-body: 16; vertebral row not enlarged, in 107 scales on body.

Colouration in preservative. After 20 years of preservation in ethanol, the specimen has more or less uniform sandy colouration. Head uniform, upper side down to height of supralabial scales sandy, underside up to height of infralabial scales dirty white; body sand-coloured, with irregular pattern of slightly darker blotches; upper fore part of tail banded dark sand-coloured, underside dirty white, from mid-tail to tip uniform dark, nearly black on both sides; belly dirty white.

Colouration in life. Similar to preserved specimen: uniform yellowish sand-coloured with shades of some slightly darker blotches. Head and forepart of body uniform yellowish-sandy, without darker pattern (see fig. 5).

Etymology. This new species is named, in deep respect, after our 'scientific father' Prof. Dr Wolfgang Böhme, deputy director and head of the Herpetology section at the Zoologisches Forschungsmuseum Alexander Koenig in Bonn, for his contributions to African herpetology for the past four decades and for the time he invested in his young students. With his encouraging lectures, discussions, excursions and fieldtrips he had a significant influence on the authors leading to their scientific current dedication with herpetological systematics, ecology and zoogeography.

Distribution. So far only known from the type locality, but an adult male was caught by a local snake hunter near Beni Kadeche (T. Holtmann pers. comm.). The new species appears currently to be endemic to Tunisia and is probably widespread in the area of Bani Kheddache.

Biology. Nearly no information is available on the biology of this species. In captivity the adult female gave birth to living young which reflects the close relationship to *C. vipera*. In respect to colouration, a sandy habitat can be assumed.

Comments. Although the species is described here based on a single voucher, more specimens were known but became apparently lost. This specimen was one of three juveniles caught together with an adult female at the type locality. The adult female had five juveniles in captivity. Additionally, an adult male was caught in the area of the type locality by a local hunter. All of these specimens have shown the described character of the unique supraocular horns.

DISCUSSION

Though described from a single specimen only, the validity of *C. boehmei* sp. n. is beyond doubt. As becomes obvious from the comparison of fine structure of body scales, the new species must be clearly assigned to the genus *Cerastes*, being distinct from burrowing *Bitis* species from southern Africa. However, the fine structure is similar to

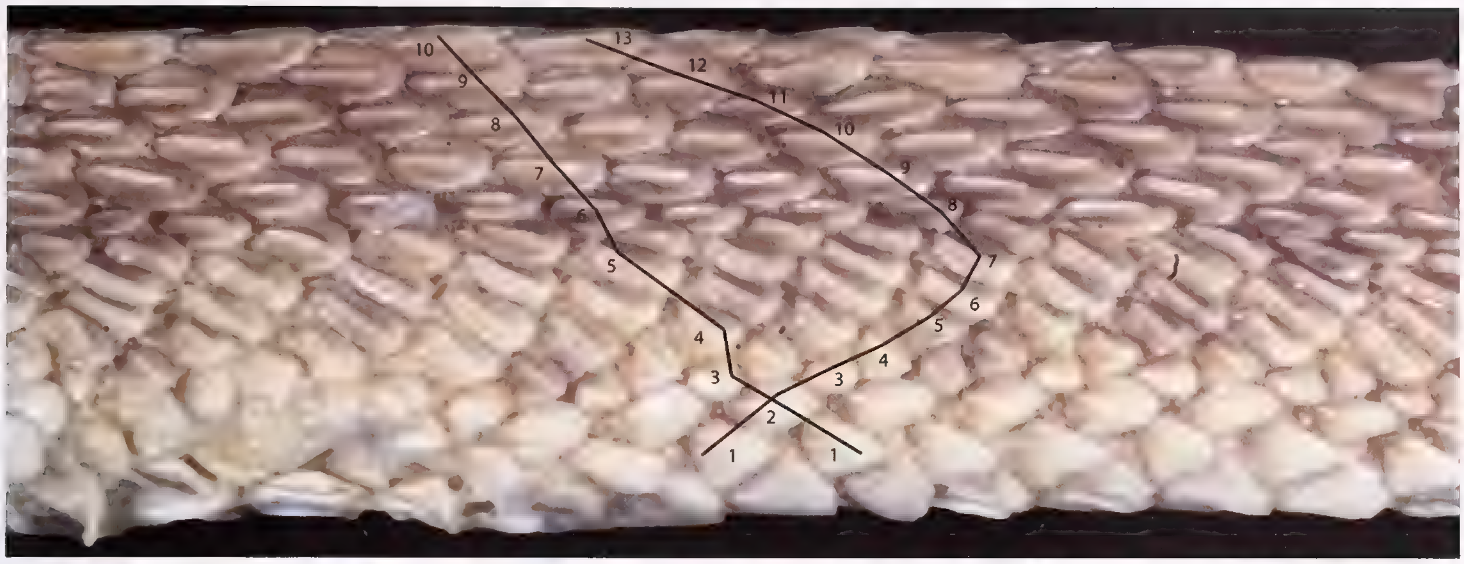

Fig. 3. Two different methods to count scale rows of dorsal scales around the midbody region of the holotype of *Cerastes boehmei* sp. n., ZFMK 58054.

both, *C. cerastes* and *C. vipera* but many other characters (e.g. shape of nostril, position of the eye, pholidosis, reproductive biology) show that the new species is more closely related to *C. vipera* than to *C. cerastes*. Accepting the results of the morphological analysis of *C. vipera* published by Jooris & Fourmy (1996) the new species has lower counts in circumocular, subcaudal, supralabial, infralabial scales and of ventral and interocular scales are on the lower limit of morphological variation in *C. vipera*. Therefore, *C. boehmei* sp. n. is clearly distinct from *C. vipera* also in pholidosis. Nevertheless, in *C. cerastes* both hornless and horned individuals are known but (a) the morphology of the "crowns" of *C. boehmei* sp. n. is clearly distinct to all other known horn structures in *Cerastes* and (b) the fact that supraocular horns or similar structures are completely unknown in *C. vipera* strengthens the validity of the new taxon as new and full species. Also Jooris & Fourmy (1996) who analysed 246 specimens comparing pholidosis in relation to a directed distribution did not mention any individuals with horn-like structures. Also none of the known synonyms of *C. vipera* possesses horns or similar structures. Nevertheless, supraocular horns as spontaneously mutation are extremely implausible. Only one case is documented where a specimen of *Macrovipera lebetina* possessed a solitary horn only on one side of the head (Böhme & Wiedl 1994).

Nevertheless, in *C. cerastes* and *C. gasperettii* hornless and horn-bearing individuals are known and a taxonomic differentiation is only known from *C. gasperettii* where the subspecies *mendelsohni* is hornless. Therefore, it can be also assumed that the supraocular scale tufts are simply a so far unknown variation within of *C. vipera*. But first of all, *C. vipera* is a well known species and e.g. Jooris & Fourmy (1996) have analysed a high number of vouchers and no single specimen is known which possess supraocular tufts and second these supraocular tufts are strongly abnormal and very distinct to the supraocular horns of *cerastes* and *gasperettii* who possess similar supraocular horns to each other.

The function of supraocular horns remains unknown. There were many speculations on the function of the horns in *Crotalus cerastes* Hallowell, 1854 from America. Klauber (1956) mentioned that they serve as radiators of heat or shaders for the eyes, whereas Cowles (1953) regarded them simply as a whim of evolution and Cohen & Myres (1970) suggest that they have the function of an eyelid protecting the snake's eye while passing through burrows. They supported this hypothesis with an ecological comparison between *C. cerastes* and *C. vipera*: the former is only known to bury itself partially and frequent rodent burrows whereas *C. vipera* is only known to bury itself fully in sand and is not reported from rodent burrows. However, another, not yet discussed, function could be a sexual recognition between the two snakes. In many reptile groups (e.g. Chamaeleonidae, Agamidae) body ornaments are known for identification during mating time. Although only males possess in most cases ornaments, it should be verified if only those population of *C. cerastes* (as this species does not strictly possess horns) bear horns, which occur directly syntopically with the hornless *C. vipera*.

Currently the new species is only known from central Tunisia and a restricted distribution can be assumed. A similar case is found in *Pseudocerastes urarachnoides* Bostanchi, Anderson, Kami & Papenfuss, 2006 which was described from a small area and a further study (Fathinia et al. 2009) found a third locality relatively close the localities of the types only.

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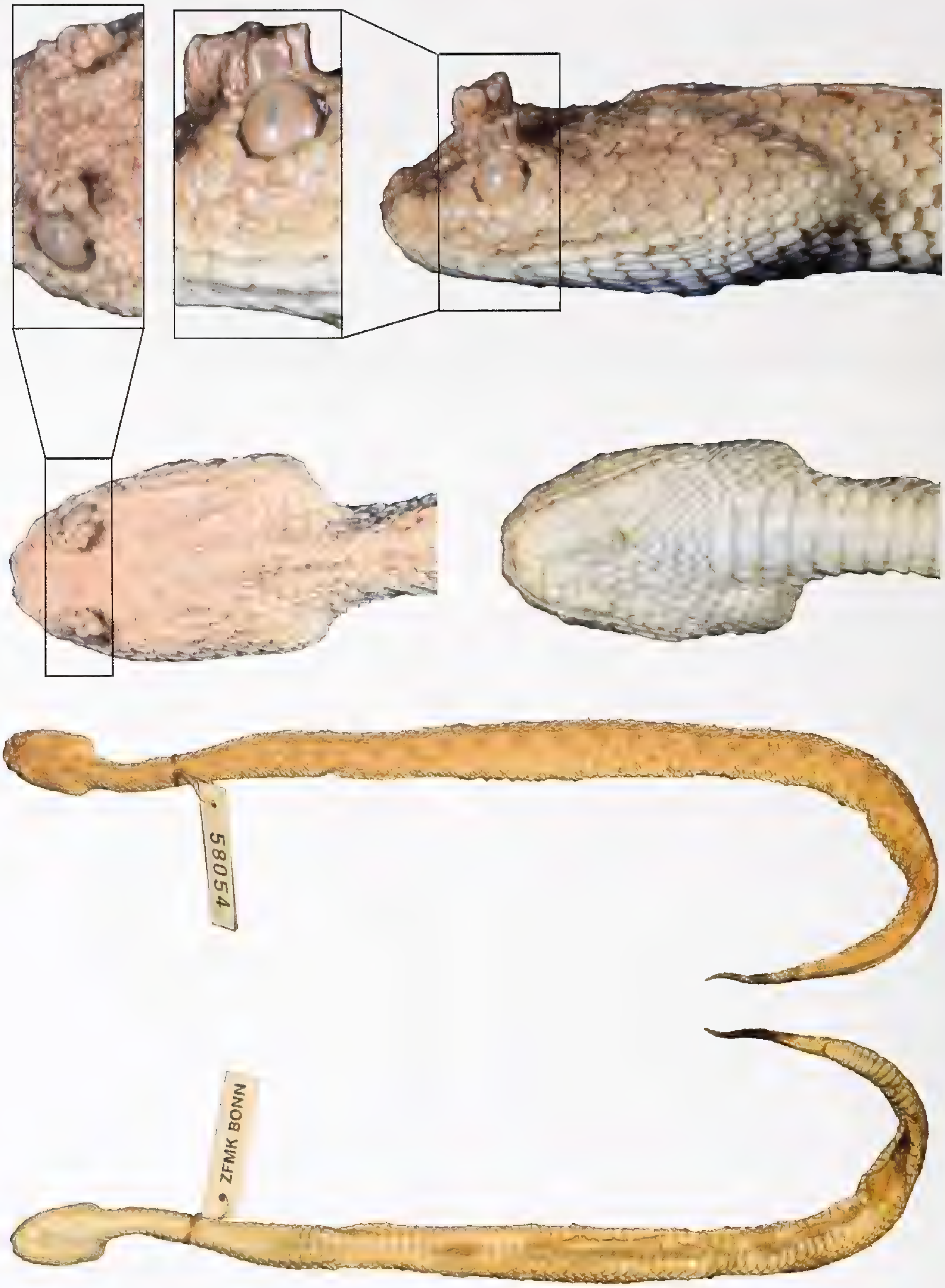

Fig. 4. Holotype of *Cerastes boehmei* sp. n.: ZFMK 58054 from SW Remada, Tunisia.

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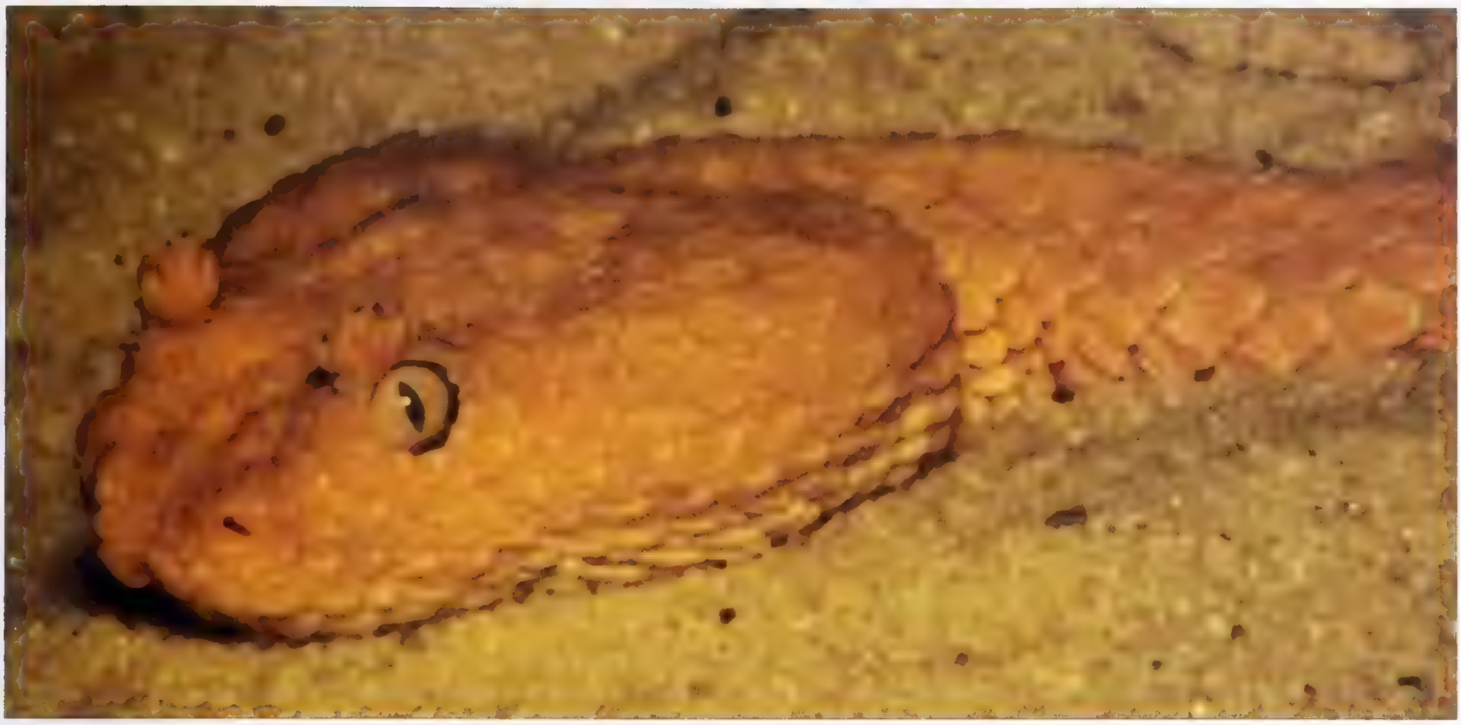

Fig. 5. Living holotype of *Cerastes boehmei* sp. n. in captivity.

The SEM analyses of dorsal scales show that *Bitis peringueyi* is different to other *Bitis* species in its secondary structure (Beyerlein 1993, and fig. 1). This structure is more or less a verrucate structure and not comparable with the cristate structure of e.g. *Bitis schneideri*, but similar to the *Cerastes* species. However, it is distinct to *Cerastes* as the imprints of borders between Clear layer cells, which are present in *Cerastes*, are not visible. Both, the *Cerastes* species and *B. peringueyi* are moreover similar in their habitats as *B. peringueyi* is one of the sand-burrowing *Bitis* species living in windblown sands of the Namib desert. Other burrowing *Bitis* like e.g. *B. schneideri* (see fig. 1) or *B. caudalis* (imaged in an unpublished thesis, see Beyerlein 1993) show the typical cristate secondary structur of *Bitis*. *B. schneideri* occurs in stable vegetated sand dunes and not like *B. peringueyi* and *Cerastes* in windblown sands. Therefore, this scale structure could be interpreted as an adaptation for this special habitat of windblown sands.

Nomenclatural comment to the nomen '*Cerastes c. karlhartli*'. Sochurek (1974) 'described' a subspecies of *C. cerastes* which he called '*C. cerastes karlhartli*'. However, the description was done in his privately published so-called 'Herpetologische Blätter', which according to art. 8.1 of the International Code of zoological Nomenclature (ICZN 1999) does not constitute a publication and therefore the description is not valid. Later, Sochurek (1979) used the name again in a summary of North African snakes but failed to provide a diagnosis, description or figure and moreover did not designate a holotype. He only mentioned the distribution and a type locality. Later, Tiedemann & Häupl (1980) accepted the name as a valid subspecies in their herpetological type catalogue of the Natural History Museum in Vienna. Werner & Sivan (1992) placed the 'subspecies' in the synonymy of *C. cerastes,* whereas Golay et al. (1993) placed it in the synonymy of *C. gasperettii*. Werner et al. (1999) did not mention the name, whereas McDiarmid et al. (1999) and Baha el Din (2006) followed Werner & Sivan (1992). However, all these authors gave neither a diagnosis nor a figure of a specimen. Therefore the name '*Cerastes cerastes karlhartli*' must be recognized as a nomen nudum.

Nomenclatural comment to the nomen *Cerastes cornutus* Boulenger, 1896. The name is used for the first time in Forskål (1775, IX), and he is often mentioned as the author of this taxon name (e.g. Schleich et al. 1996, Baha el Din 2006). But Petrus Forskål died during the Danish Arabia expedition, and Carsten Niebuhr published Forskål's results after his death. Nevertheless, the name is part of a summary about different species which Forskål wanted to describe, but finally never managed to do before his untimely death. Additionally, this nomen is not accompanied by either a description or a drawing. Therefore, Boulenger (1896) who was the first to use the name together with a description must be recognised as the author of *Cerastes cornutus*, despite the fact that Boulenger himself mentions Forskål as the author of this species.

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The taxonomic history of the Linnean genus *Lacerta* (Squamata: Sauria: Lacertidae) in the mirror of book-illustration

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Abstract. The taxonomic history of the Linnean genus *Lacerta* illustrates the general taxonomic history in herpetology and can be visualized by the history of book illustration. There is a cohesive pattern in lumping *Lacerta* (Linnaeus, 1758; comprising lizards, crocodiles and salamanders; expanding to almost 100 species in Shaw, 1802) and splitting (Laurenti, 1768; comprising among others his new genus *Seps*, a part of Linnaeus' *Lacerta*), since the creation of binominal nomenclature by Linnaeus, and proceeding above all to the controversy of Boulenger and Méhely after 1900. These wavelike advances through the centuries are also characterized by a slow consolidation of the higher systematic categories (class-order-family-subfamily, etc.) and by a gradual reduction of the term *Lacerta* to almost the species level. This development ended now in an enormous generic and specific splitting within the family Lacertidae (Arnold et al. 2007), mainly based upon mitochondrial DNA research. The remaining "true" *Lacerta* comprises at present only half a dozen species, all of them close relatives of the type species, *Lacerta agilis*.

There is an historical interdepency between verbal descriptions and illustrations in the taxonomic advances of the genus *Lacerta*. The first illustrations of lizards (in the 16th century) are in equal measure characterized by the lack of systematic insight and the lack of technical options. Copper engravings (handcoloured) were used a little later. Since the end of the 18th century, new techniques accompanied and immensely facilitated a better recognisability of taxa: wood engravings – lithographs – chromolithographs – photos – modern digital colour photographs. The better understanding of the diagnostic scale structures called for their schematic depiction, and a schema of the dorsal drawing pattern was established. Diagrams for identification keys and/or of the phylogenetic relationships have become an indispensable part of modern taxonomic work. On the contrary, the genetic revolution of the last 20 years caused a great loss in importance of morphological characters, whereas top-quality digitalized coloured photos have shifted their importance mainly to popular publications on ecology, ethology, field herpetology and terraristic studies.

Keywords. Genus *Lacerta*; history; interdepency text/illustrations.

1. INTRODUCTION: SOME COMMENTS ON THE ZOOLOGICAL TERM *GENUS*

The history of the Linnean genus *Lacerta* is likewise a history of the term "genus". As Mayr et al. stated in 1953, the genus is a collective taxonomic unit consisting of a number of similar or related species. It is distinguished from all other higher categories by being recognized in the scientific name. The nomenclature proposed in Linnaeus' Systema Naturae (1758; animals) is binominal, consisting of two names, each with its own function. The functions which Linnaeus visualized for the components of the scientific name are diametrally opposite. The specific name signifies singularity and distinctness; the generic name calls attention to the existence of a group of similar or related species – it relieves the memory (Mayr et al. 1953: 48).

Even before Linnaeus there was a recognition of the categories *genus* and *species*. So, Plato definitely recognized two categories, the genus ("genos") and the species ("eidos"), and so did his pupil Aristotle. The naturalists of the pre-Linnean era were not consistent in the Latin names they gave to plants and animals. These names ranged all the way from uninominals (a generic name only), and binominals (a generic and a simple trivial) to polynominals (a generic name with several trivial epithets). The reason for this confusion was that they tried to combine two different functions in the name: naming (in the restricted sense of the word) and describing (Mayr et al. 1953: 202; see the legends in the images of Gessner and Aldrovandi Figs 2 and 3 hoc loco).

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An objective criterion for the generic rank does not exist equivalent to the biological species concept ("reproductive isolation") in species systematics (see Mayr 1984: 141, 219; Jahn 2004: 237, 397; Joger 1996) as a criterion. It is therefore impossible to give an objective definition of the genus. So Mayr et al. (1953: 48) came to the following conclusion: "A genus is a systematic category including one species or a group of species of presumably common origin, which is separated from other similar units by a decided gap". They suggest for practical reasons that the size of the gap be in inverse ratio to the size of the unit; the latter qualification should prevent the recognition of unjustified monotypical genera.

The general view on the definition of the category genus has not changed much since then, contrary to the different species concepts (e.g. Joger 1996). Even Mayr et al. (1953) had attenuated their clause appearing so strict ("An objective criterion does not exist ...."; p. 48) when discussing the presence of an "ecological niche" (p. 50) between genera. Later on Dubois (1988) and recently Dubois & Bour (2010) have extensively discussed the demand of "hybridizability" as a criterion for the definition of genera and subgenera. Additionally, the genetic revolution in taxonomy since the 1990s has decidedly consolidated the phylogenetic trees. So Speybroeck et al. (2010), in the introduction to their recent species list of the European herpetofauna, come to the decision: "As a distinct genus, we tend to recognize monophyletic clades that are genetically as divergent as other widely accepted genera in the same group. This is usually the approach employed by authors of scientific papers....". As a conclusion one might assert, that it was molecular biology which gave rise to a still continuing revolution in herpetological taxonomy, and – above all – to an enormous generic splitting, be it of the old Linnean genera *Testudo*, *Rana, Coluber,* or *Lacerta,* the latter being discussed here.

2. A BRIEF HISTORY OF THE LINNEAN GENUS *LACERTA*

2.1 The "lumper" Linnaeus (1758 / 1766) and his followers

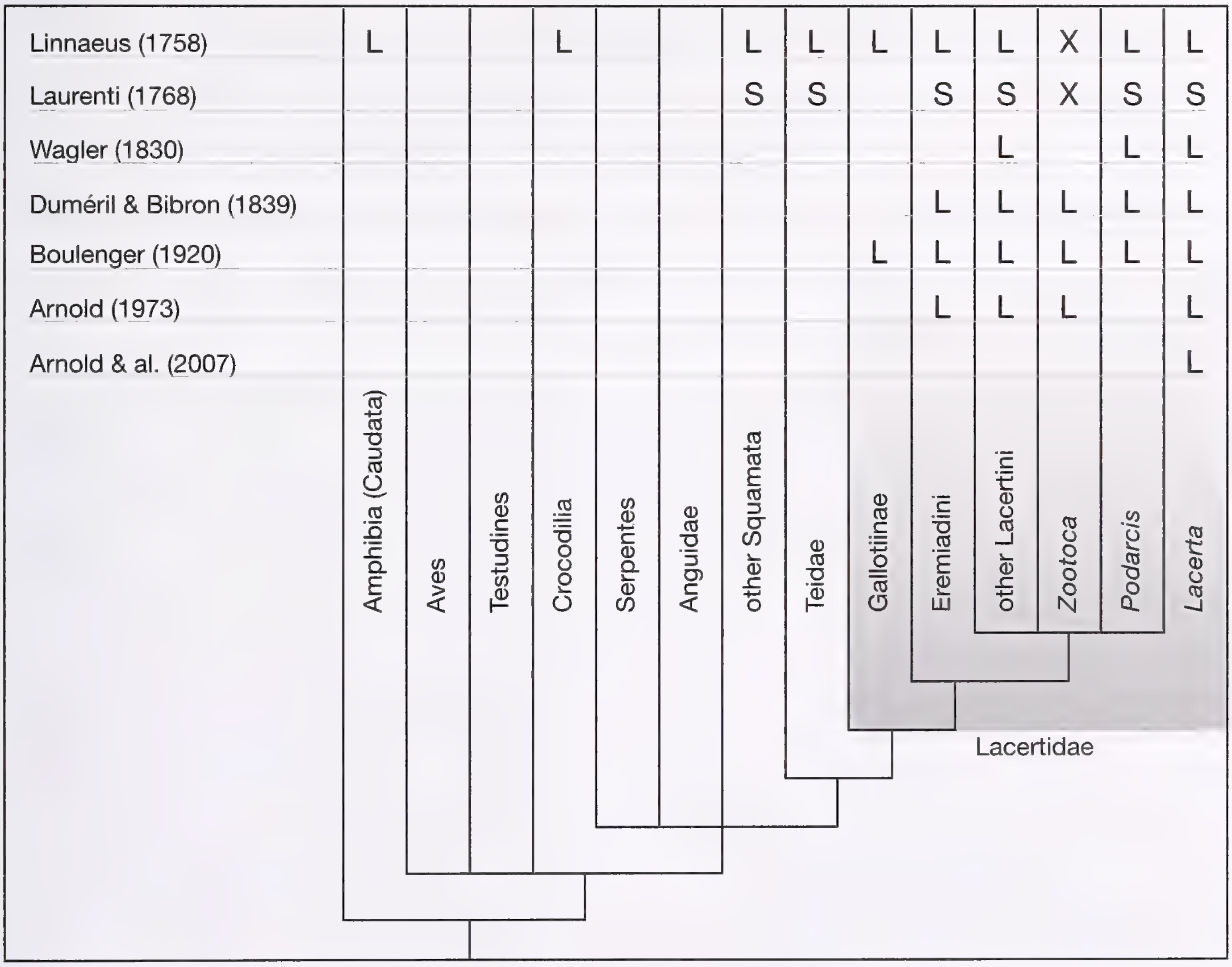
The history of the genus *Lacerta* reflects also a history of zoological terms and categories, which can be dealt here only with its basic intentions. The word "Lacerta" (or the male gender "Lacertus") is of Latin origin. One of its three meanings is the linguistically derived English term "lizard". In this sense it is traceable in the Historia Naturalis of Plinius or in some works of the classic Latin poets Ovidius and Virgilius (Scheller, 1796). Since the era of renaissance this term was renewed by natural scientists in both the male and female gender (see Figs 1, 2, 4). Thus the term *Lacerta / Lacertus* had a long history before Linnaeus began to use it in the different editons of his "Systema Naturae" since 1735.

Linnaeus (or "Linné" after nobilitation), in his famous 10th edition of 1758, divided the class "Amphibia" into three orders: I. Reptiles, II. Serpentes, III. Nantes. The "Reptiles" comprise the four genera *Testudo, Draco, Lacerta, Rana*; the Serpentes comprise the six genera *Crotalus, Boa, Coluber, Anguis, Amphibaena, Caecilia*. The Nantes comprise six genera, all of them being transferred later on into the class Pisces. The Linnean *Rana*, parts of *Lacerta* and *Caecilia* constitute the current class Amphibia whereas the other genera in Linné's orders Reptiles and Serpentes are comprised in the present-day – polyphyletic – Reptilia. Linnaeus' (1758/1766) large genus *Lacerta* is an aggregation of 43/49 species, e.g. comprising the current Lacertidae (type species of Linnaeus' *Lacerta* is *Lacerta agilis* by later designation in Fitzinger 1843: 20), many other Reptile orders (like the crocodylia) and families, and even amphibians (e.g., salamanders; see Fig. 1). His genus *Lacerta* is encompassed by the diagnosis "Corpus, tetrapodum, caudatum, nudum" (body with four legs, caudate, "naked"; the latter characterization being completely incomprehensible, since his genus *Rana* is also characterized to be "naked"!). It seems that Linnaeus did not misjudge completely the heterogenity of his genus *Lacerta*. He tried to resolve the problem by species groups, characterized by short diagnoses and different stars. So his *Lacerta agilis* is within a group characterized by "** Cauda verticillata" (Tail round) and the group with the fire salamander, "*Lacerta salamandra",* is characterized by "***** Palmis tetradactylis; Corpore alepidoto nudo" (fore legs with four toes; body without scutes, naked). Nevertheless the newt "*Lacerta vulgaris"* (number 25; now: *Lissotriton vulgaris*) is grouped together with geckos and skinks.

Gmelin (1789) was formally a follower of Linnaeus, but he undermined his concept in the so called 13th edition of Linné's "Systema Naturae" where he accumulated the number of *Lacerta* species up to 77. Gmelin introduced eleven species groups within *Lacerta,* characterized by short diagnoses and mostly (but not always!) naming them (nominative plural of a main species being included, like "Salamandrae" with five stars (*****), comprising the Linnean *Lacerta salamandra*, No. 47) – or his "Ameivae s. Sepes" ("s." = "sive"; English: "or") comprising the Linnean *Lacerta agilis* – or the "Lacerti" (with nine stars) covering current tailed amphibians and reptiles, except lacertids, like the newt "*Lacerta vulgaris*" (now: *Lissotriton vulgaris* which is therefore not a part of his "Salamandrae"!). It is clearly noticeable that Gmelin, following Linnaeus, avoided dividing the genus *Lacerta* formally, unlike Laurenti (1768) had executed. The non-scientific reasons may have been similar as described below in the discussion on Shaw.

Donndorf (1798) followed Gmelin (1789). He used the German terms “Geschlecht und Gattung” instead of “Gattung und Art” (genus and species; “Vorrede” p. 5). In his genus *Lacerta* Gmelin’s system with eleven species groups, characterized by eleven stars, is comprised; he added however 14 newer species (“neuere Gattungen”) within these species groups and nine species of undetermined species groups.

Shaw’s (1802) General Zoology (vol. III, part III, Amphibia) is the last of the great encyclopaedias around 1800 which formally retains the generic name *Lacerta* in the broad Linnean sense. Its number of species has increased up to 86. Like the preceding encyclopaedias Shaw divided *Lacerta* into nine “sections or sets” giving them English names. He admitted however: “The above divisions neither are, nor can be, perfectly precise…” His “4. Lizards proper “ comprised also the current day Lacertidae, among them the ”Green lizard” “*Lacerta agilis*” taking first place. Smith & David (1999: 12, 13), when discussing the taxonomic situation then, drew the conclusion: “The rudimentary level of understanding of herpetological classification in Shaw’s time is admirably exemplified by his treatment of the Division Lacertae, containing only two genera – *Draco* and *Lacerta* – that are extremely disparate in diversity. Nevertheless, Shaw was much more aware of the diversity and affinities of members of his genus *Lacerta* than is apparent in the assignment to one genus, inasmuch as he recognized nine distinct groups. To us it seems strange that such diversity was not reflected taxonomically when the relatively minor specialization of *Draco* received such emphasis. However, although Shaw boldly named new species or changed names, he reflected the trepidation widely shared at that time among his colleagues in splitting Linnean genera. Change then, as



	Amphibia (Caudata)	Aves	Testudines	Crocodilia	Serpentes	Anguidae	other Squamata	Teidae	Gallotiinae	Eremiadini	other Lacertini	*Zootoca*	*Podarcis*	*Lacerta*
Linnaeus (1758)	L			L			L	L	L	L	L	X	L	L
Laurenti (1768)							S	S		S	S	X	S	S
Wagler (1830)											L		L	L
Duméril & Bibron (1839)										L	L	L	L	L
Boulenger (1920)									L	L	L	L	L	L
Arnold (1973)										L	L	L		L
Arnold & al. (2007)														L

Fig. 1. Overview of the gradual reduction of the Linnean genus *Lacerta* (Laurenti’s genus *Seps* respectively) from selected monographs: Linnaeus (1758) – Laurenti (1768) – Wagler (1830) – Duméril & Bibron (1839) – Boulenger (1920) – Arnold (1973) - Arnold et al. (2007: fig. 20); displayed upon a current phylogenetic tree (strongly simplified; from Dawkins, 2008, figs. p. 366, 422, 462; Arnold et al. 2007 figs.). The symbols ***L*** or ***S*** make clear a quotation of “*Lacerta*” (or “*Seps*” by Laurenti) within a given current systematical unit; ***X*** (no species from this group being described then).

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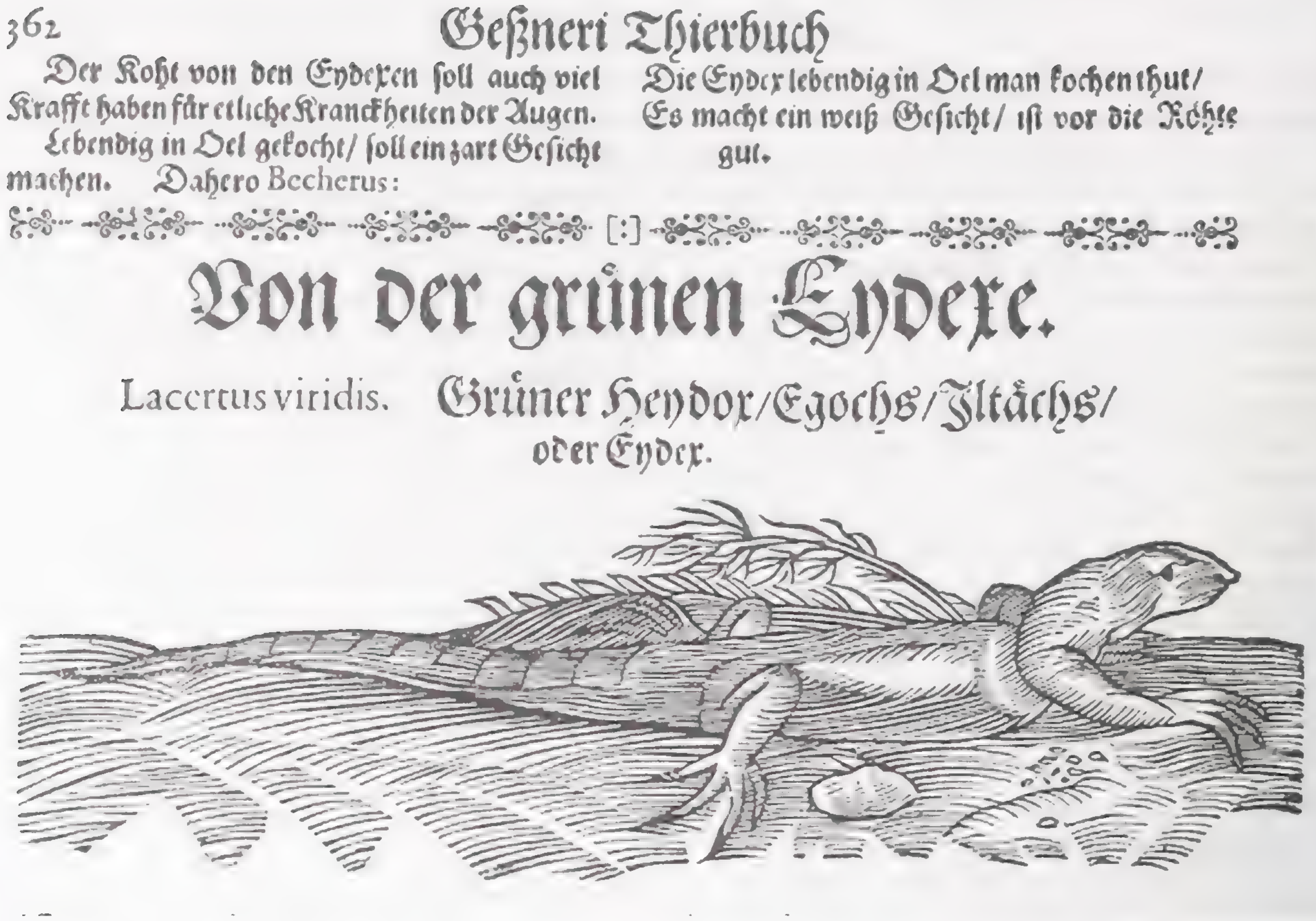

362 Geßneri Thierbuch

Der Koht von den Eydexen ſoll auch viel Krafft haben für etliche Kranckheiten der Augen.

Lebendig in Oel gekocht/ ſoll ein zart Geſicht machen. Dahero Becherus:

Die Eydex lebendig in Oel man kochen thut/
Es macht ein weiß Geſicht/ iſt vor die Röhte gut.

Von der grünen Eydexe.

Lacertus viridis. Grüner Heydox/Egochs/Iltächs/ oder Eydex.

Fig. 2. "*Lacertus viridis*" from Gessner's (1671) last edition, the so called "Frankfurter Ausgabe". Wood cut.- The eye-catching bars across the tail indicate the whorls typical for a Lacertid tail. The text consists of medical and cosmetic advices, the latter in the form of a verse. The different insights of a painter and a mere engraver as well as the different qualities of a water colour compared with an engraving are shown by a comparison to an Aldrovandi image (Fig. 3).

now, came slowly. Shaw worked in a surprisingly substantial intellectual milieu of peers who would look critically at any change from established authority". A comparable thoughtfulness seems to have been widespread in science – at least then (compare the situation of N.M. Oppel after his studies in Paris, being surrounded by "natural philosophers" in Munich since 1811; Schmidtler 2009: 509; Figs 16, 17 hoc loco).

The "Histoire Naturelle des Quadrupèdes Ovipares et des Serpens" by Lacepède (1788/89) is a milestone in the history of natural science. It highlights the beginning of the acceptance of Linnaeus's binominal system also in France, then leading in natural science. Up to that time the well known scientific controversies of Linnaeus (1708–1779) and Buffon (1708–1788) had prevented to a large extent the application of Latin binominal names in the French zoological and botanical literature, especially in the dozens of volumes of Buffon's "Histoire Naturelle" having appeared since 1750. The acceptance of Linnaeus' binominal system by Lacepède appears admittedly in a rather hesitant and concealed manner. It turns up only in the gigantic Latin "Synopsis methodica Quadrupedum oviparorum" beside the French "Table méthodique des Quadrupèdes ovipares" (see the elaborate description in David et al. 2002: Fig. 2). Here Lacepède accepted two classes. His first class ("Quadrupedes ovipari caudati") comprises two genera, *Testudo* and *Lacertus* ("Corpus absque testa"). The latter, with 56 species, is divided into eight divisions ("divisio") which are each described shortly, but not named. As Spix (1811: 342) pointed out there is however a contradiction between Lacepède's (1788) zoological findings in the text and the construction in the "Table méthodique" when stating that the salamanders are nearly related with the frogs. He accepted two current lacertid species in his third division (*Lacertus cinereus* and *Lacertus viridis*; both highly collective groupings, comprising among others the current genera *Lacerta / Timon* and *Podarcis / Zootoca* respectively; see also Schmidtler & Böhme, in prep.). The six species of salamanders are, contrary to Linnaeus and Gmelin, concentrated in one division ("VIII. Divisio"). It may be noted that the name with the male gender "*Lacertus*" Lacepède, 1788 is regarded to be an unjustified emendation

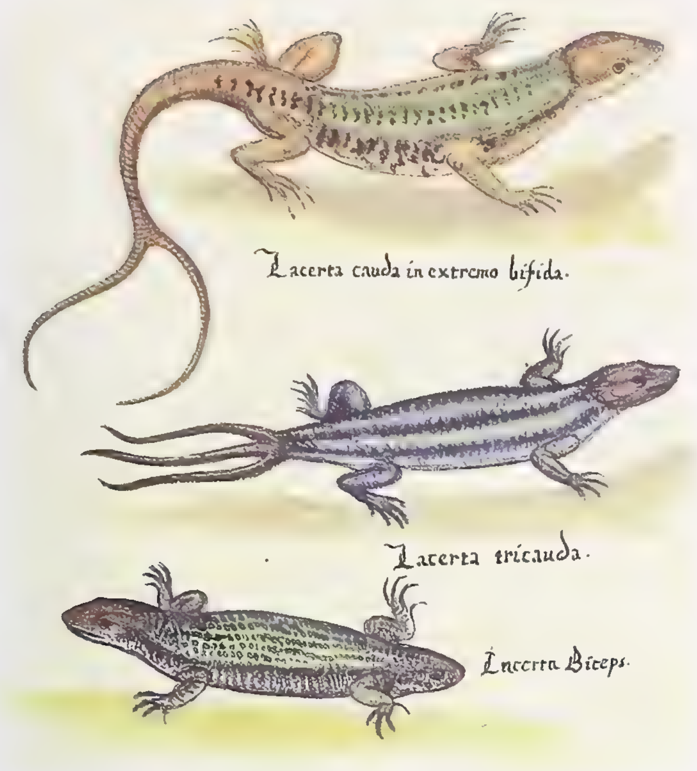
Lacerta cauda in extremo bifida.
Lacerta tricauda.
Lacerta Biceps.

Fig. 3. *Podarcis siculus* ssp. From the collection of Aldrovandi's natural history images (16th century), see also Ceregato & Alessandrini (2007: fig. 462 upper part) and Delfino & Ceregato (2008). Water colour (Tempera). – The shapes and colours of lizards are excellently painted but the head shields are scarcely indicated. The naming of tail anomalies (especially *Lacerta* "biceps"!!!) reveals the lack of a species concept and the lack of a preset nomenclatural terminology. See chapter 3.2.

of *Lacerta* Linnaeus, 1758 (see David et al. 2002: 24). Lacepède's volume 1 and volume 2 (on the snakes) were rejected in general as a non-binominal work. This opinion remained heavily controversial (see David et al. 2002: 22; Dubois & Bour 2010). Anyway, one year later many species were adopted by Bonnaterre (1789) who has therefore become the correct author of many of Lacepède's names not being available. On Bonnaterre's *Lacerta* see more in chapter 2.2.

As obvious from the title, Bechstein's encyclopedia (1800–1802), "Herrn De la Cepede's Naturgeschichte der Amphibien" is first of all a translation from Lacepède's (1788 / 89) Histoire Naturelle, but comprising many additions. Bechstein used German terms. In his "Methodische Übersicht der eyerlegenden vierfüßigen Thiere" he translated Lacepède's system with the terms Classe, Gattung (genus) and Art (species), inserting the term "Familie", apparently in the sense of a species group below his "Gattung" in some genera, like the "Eidechsen" (lizards). He neglected Linnaeus' Latin binominal teminology to a large extent. His terminological system concerning the category "Art" (species) is inconsistent and confusing. In his "Zweyte Gattung, dritte Familie" (vol. II, like in Lacepède 1788) some current Lacertidae ("*L. cinereus*, die graue Eidechse" and "*L. viridis*, die grüne Eidechse") are comprised. He gave an excellent picture of the "Graue Eidechse / *L. cinereus*" (vol. II, Taf. 1; depicting the male and the female of a present-day *Lacerta agilis*), and demonstrating thereby that this important taxon was then differently understood in different European countries (see

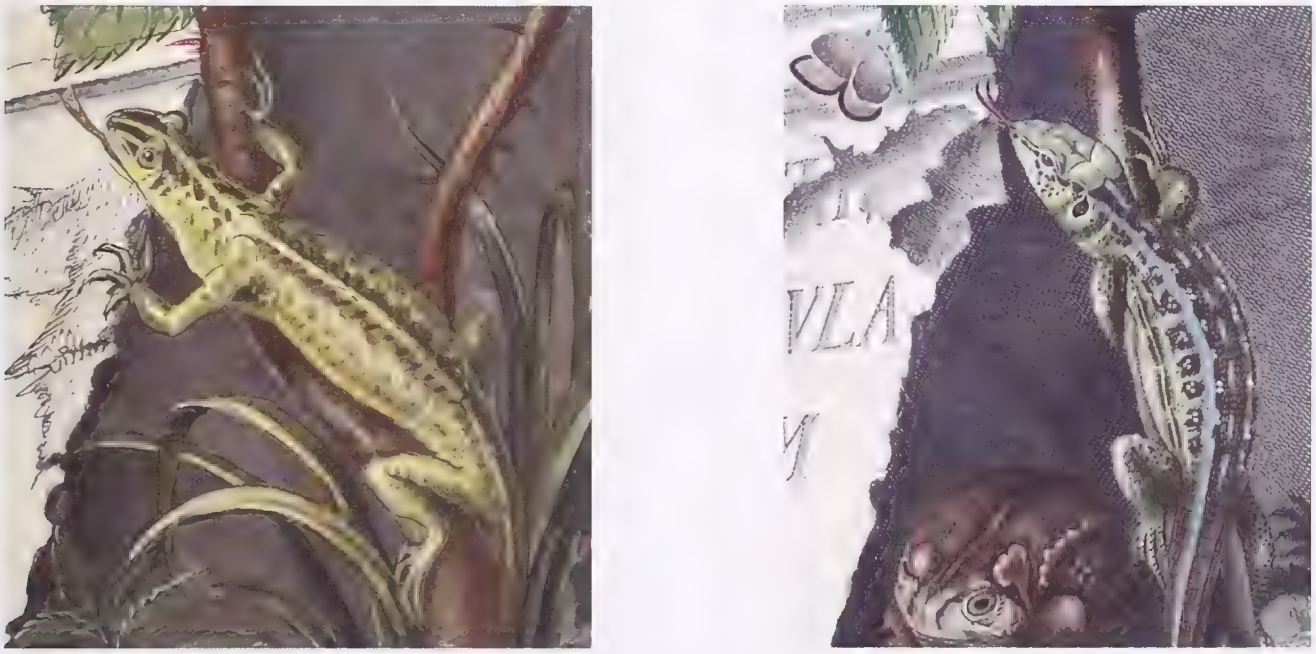

Fig. 4. *Lacerta agilis* (male). Left figure: Draft of the right figure; drawer Rösel von Rosenhof (Cod. Icon. 48, Bayerische Staatsbibliothek München; before 1758). Water colour. – Right figure: Frontispiece in Rösel v. Rosenhof (1758). Hand coloured engraving.- The changes in scientific insight by the famous drawer and natural scientist Rösel mirror as well his personal "metamorphosis" as the changes in general views in differentiating a "salamander" (left: with its nude skin!) from a lizard (right: with its lifelike scaly skin and pileus scutes; but: occipital and interparietal scutes are still lacking!). Both, salamanders and lizards, became in the same year parts of the Linnean genus *Lacerta*.

also Schmidtler 2004; Schmidtler & Böhme in prep.). In his “Anhang” (additions; vol. II, 297–325) however, Bechstein on the one hand accepted the modern binominal terminology of Laurenti (1768) and Schneider (1799; e.g. *Stellio phylluros*, p. 307) or used Gmelin’s (1789: 1060) Latin species group terms, (p. 311; like *Stelliones* = “Spiegeleidechsen”).

2.2. Early generic splitting after Linnaeus

Laurenti (1768) was the first to subdivide the Linnean genera of amphibians and reptiles (Testudines excluded) in a comprehensive work, especially Linnaeus’ large genera *Lacerta* and *Coluber*. Laurenti totally suppressed the name *Lacerta*, but established instead of 11 new genera within his order II “Gradientia” (see Kuzmin 2005: 246), among them “*Seps*” comprising also the current species of Central European *Lacerta* and *Podarcis* and some of their synonyms (see chapter 2.4; see Fig. 1). After Stejneger’s (1936) type species designation (*Seps caerulescens* = *Lacerta agilis*; see also Dubois 2010; and Fig. 6 hoc loco) Laurenti’s *Seps* became a junior synonym of *Lacerta*. *Seps* Laurenti comprised after all only four current families, all within the Squamata (Lacertidae, Scincidae, Teiidae, Gymnophthalmidae) and appears therefore much more restricted than the Linnean *Lacerta*.

Laurenti’s splitting had still an earlier forerunner in Garsault’s (1764) long forgotten and just rediscovered work “Les Figures des Plantes et Animaux” here concerning in particular the French herpetofauna around Paris in ten plates (see Welter-Schultes et al. 2008, 2009; Dubois & Bour 2010; Fig. 5 hoc loco). Garsault (1764) used the species names *Lacertus terrestris* (now: *Podarcis muralis* (Laurenti); nomen conservandum), *Lacertus viridis* (now: *Lacerta bilineata* Daudin; nomen conservandum), the genus names *Scincus, Salamandra* (with the French name “salamandre” behind; depicting *Salamandra salamandra terrestris* Bonnaterre). A certain systematic unstableness is however unmistakable when depicting the crested newt (today *Triturus cristatus* (Laurenti), nomen conservandum) under the Latin nomen *Lacertus aquatilis,* but simultaneously under its French name “Salamandre d’eau”.

Valmont de Bomare in the second issue of his “Dictionnaire d’Histoire Naturelle” (1767/68) added for the first time Latin names to the French names. There appear likewise considerable systematic inconsequences: On the one hand, under the key word and generic name “Lézard / *Lac-*

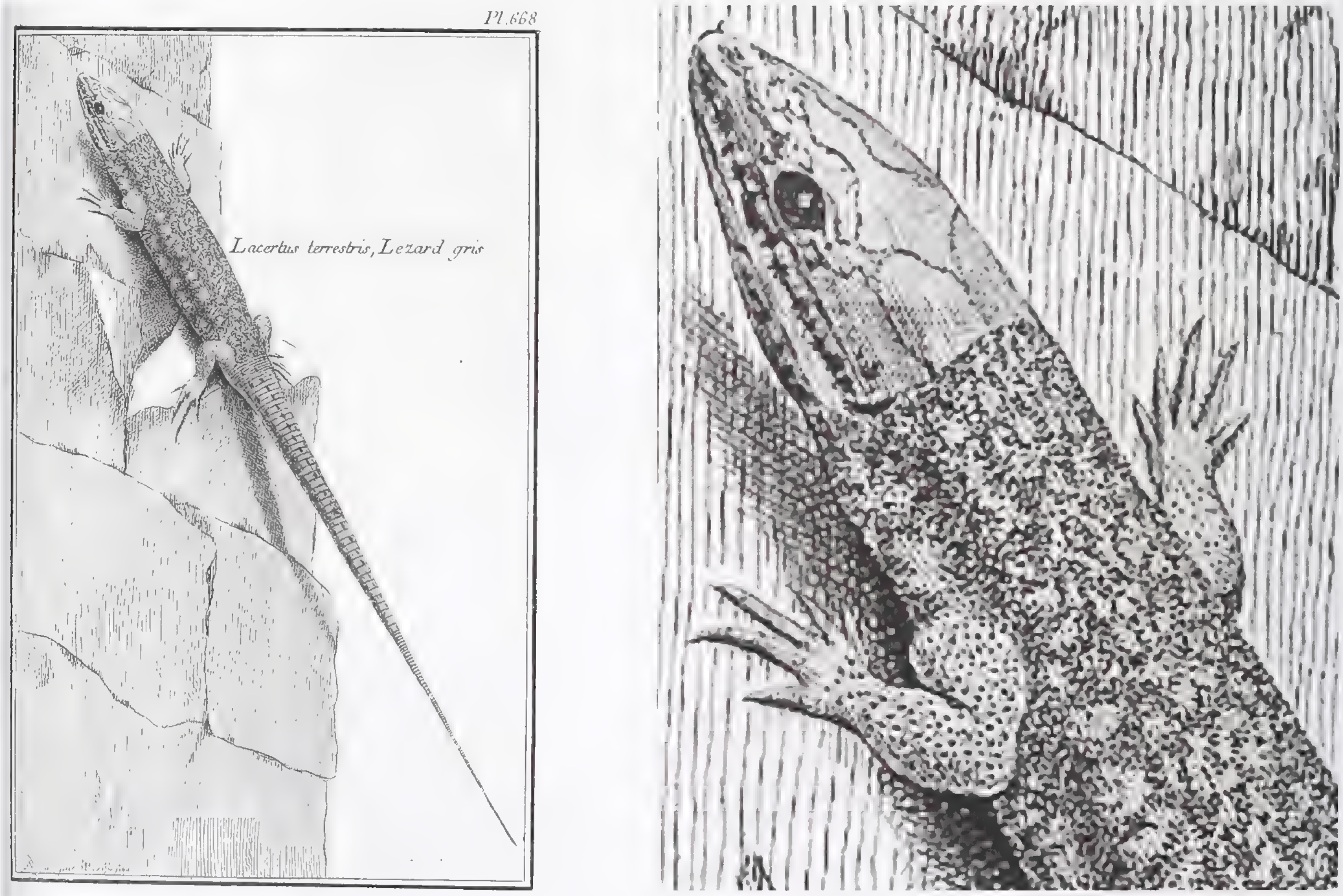

Fig. 5. “*Lacertus terrestris*” (= *Podarcis muralis*; western subspecies) from Garsault (1764), a forerunner of Laurenti (1768), having been rediscovered in the last years (see Dubois & Bour 2010). Copper engraving. – The pattern of the upper head scutellation (right figure) is not yet perfect; the frontal and postfrontals are not executed within the central part of the pileus.

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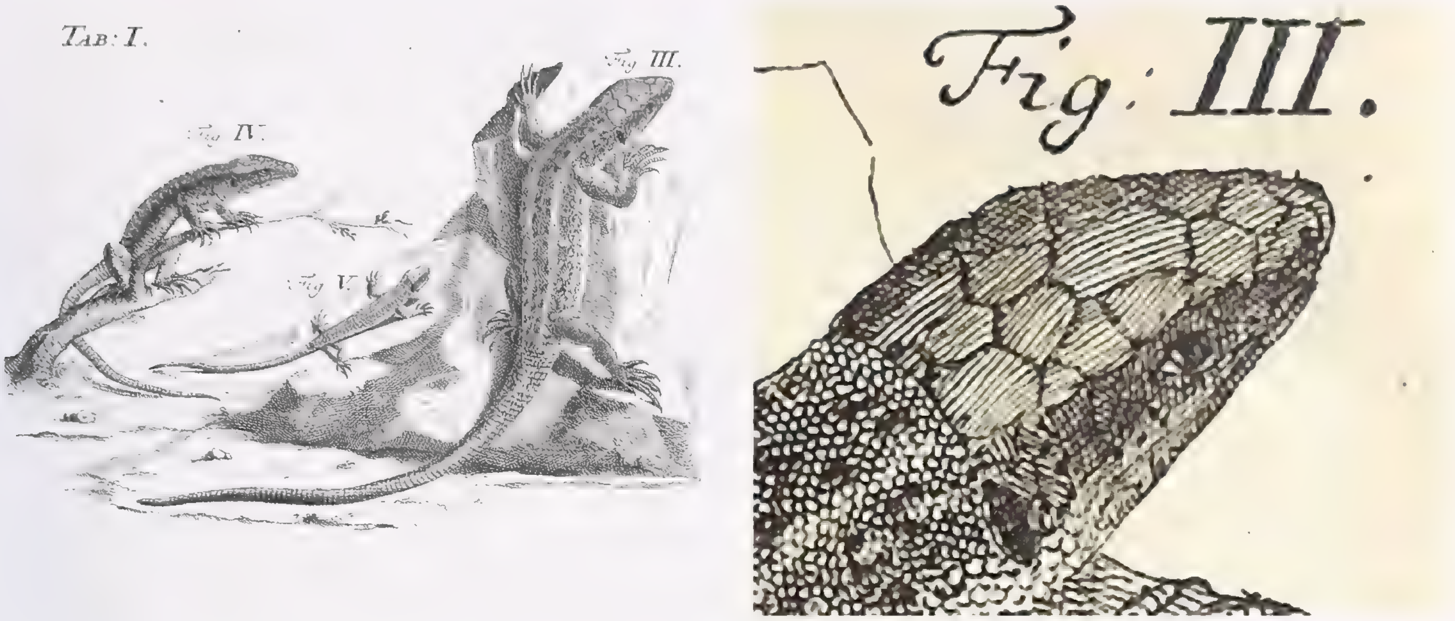

Tab: I.
Fig III.
Fig IV.
Fig V.
Fig: III.

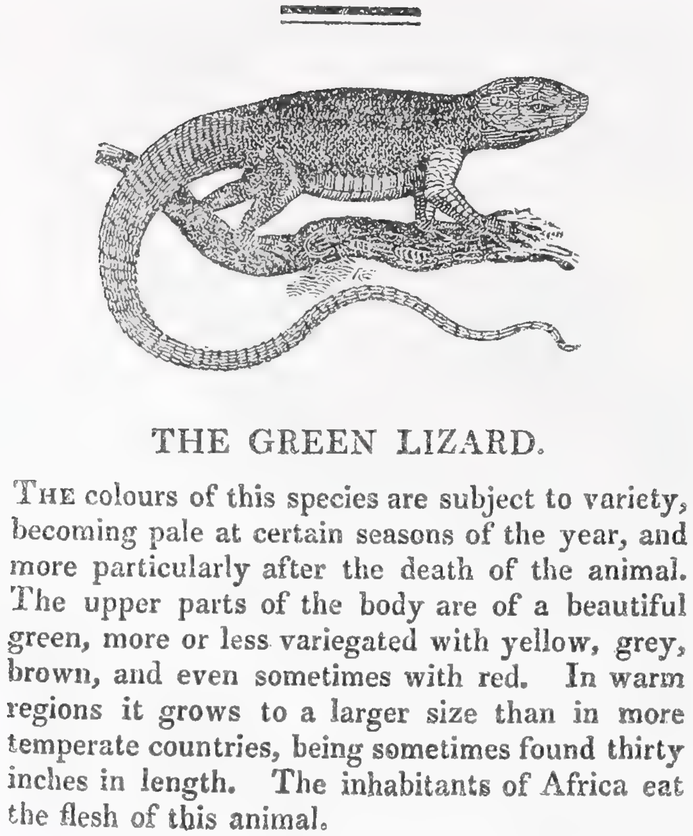
Fig. 6. *Seps caerulescens* (= *Lacerta agilis*; Fig. III), *Seps muralis* (= *Podarcis muralis*; Fig. IV), *Seps argus* = a juvenile *Lacerta agilis*; Fig. V). From Laurenti (1768: Tab. I, upper part). Copper engraving. – Laurenti's (1768: Tab.I, fig.III) *Seps caerulescens* has accomplished perfection for the first time in the history of a lacertid engraving: The arrangement and shape of all of the pileus scutes are accurate. In equal measure the dorsal pattern is very representative for the species. This figure is all the more outstanding, as Laurenti himself was obviously not yet aware of the enormous impact of head scutellation in species recognition. So it was the exactness of the drawer and the engraver who were solely responsible for the quality of the figure. Developments like these demonstrate the prospective relevance of naturalistic figures in book illustration for the scientific progress in reptile systematics about 1800. Otherwise, the quality of the smaller figures IV and V is considerably lower and does scarcely contribute to species recognition.

ertus" (Vol. III, p. 548, 1768), all the "amphibian species" in Linnaeus' (1758) sense are understood. On the other hand, under the keyword Salamandre / *Salamandra,* Valmont de Bomare (vol. V, p. 441, 1767) described only "real" salamanders, and explicitely the two species *Salamandra terrestris* (currently: *Salamandra salamandra terrestris* Bonnaterre) and *Salamandra aquatica* (apparently a collective species comprising some current species of water newts, especially *Triturus cristatus*). This dictionary was however suppressed by the ICZN (Anonymus 1925; Dubois & Bour 2010), its nomenclature not being always binominal for species.

Although Bonnaterre (1789; see also 2.1), often misunderstood as a mere copyist of Lacepède, took over many details from Lacepède (1788) in his "Tableau Encyclopédique", he did not follow him (nor indirectly Linnaeus) in his generic lumping. On the contrary, he widely accepted the generic splitting by Laurenti. His first class ("Reptilia ecaudata") comprised the three genera of Laurenti: *Rana, Hyla, Bufo,* whereas his second class (Reptilia caudata) with seven genera approached Laurenti's second order (less genera indeed), excluding the snakes as well, but comprising the turtles (*Testudo*). Bonnaterre's *Lacerta* comprised 52 species, among them still some of Laurenti's new "lizard" genera, like *Basiliscus, Iguana, Ameiva, Stellio.* Bonnaterre suppressed Laurenti's generic name *Seps* and the current Lacertidae are comprised in his genus *Lacerta*. He also doubted the validity of some of Laurenti's new species (e.g. *Seps caerulescens,* now *Lacerta agilis*).

Latreille in Sonnini & Latreille (1801) in gross terms accepted the generic systematics of Laurenti (1768). Some of Laurenti's species of the new genus *Seps* were included in the "IIIe genre Lézard, *Lacerta*". Latreille anticipated many of Daudin's (1801–1803; see chapter 3.3) descriptions and took the opportunity to thank him for his communications (1801, vol. 1, p. 215; "M. Daudin...a eu l'amitié de me communiquer, par extrait, les descriptions qu'il a faites de plusieurs reptiles de la famille des lézards... Il me sera doux, en le citant, de lui payer à la fois le tribute de mon estime et celui de l'amitié"). Harper (1940) named this procedure a certain sort of piracy.

In early regional faunas, which do not cover the whole family of lacertids, the acceptance of Linnaeus' lumping or Laurenti's splitting was heterogenous. Being one of the first authors, Schrank (1784 and 1798) completely adopted Laurenti's genera (e.g. "*Salamandra atra*" Laurenti, "*Seps viridis*" Laurenti), whereas Razoumowsky (1789) or Wolf in Sturm (1799, 1802, 1805) were using Linnaeus' terminology system (e.g. "*Lacerta agilis*" Linnaeus or *Lacerta paradoxa s. helvetica*" (n.sp.; now the newt *Lis-*



THE GREEN LIZARD.

THE colours of this species are subject to variety, becoming pale at certain seasons of the year, and more particularly after the death of the animal. The upper parts of the body are of a beautiful green, more or less variegated with yellow, grey, brown, and even sometimes with red. In warm regions it grows to a larger size than in more temperate countries, being sometimes found thirty inches in length. The inhabitants of Africa eat the flesh of this animal.

Fig. 7. "Green lizard" (= *Lacerta viridis*); probably the first lizard in the renewed wood cut technique by Bewick (1809 – 1816; "wood engraving"; cf. Dance, 1989, Schmidtler, 2007). As usual then, engravings of the "abhorrent" reptiles (so Linnaeus 1758:194) were significantly of a lower quality than the birds or mammals (cf. the images in Bewick 1791). Nevertheless this green lizard is recognizable here. It was a great advantage of this printing technique that the images could be printed together with the text upon the same page (unlike copper engravings or lithographs - these upon separate plates). So, later on, wood engravings proved to be adequate for the popular small English "chap books", or the German "Naturgeschichten". This kind of letter press was also often used for schematic figures in a text page.

sotriton helveticus) in the former; "*Lacerta atra*" (Laurenti), and "*Lacerta agilis*" Linnaeus in the latter. In contrast Koch in Sturm (1828) made use of Laurenti's generic names ("*Seps stellatus*" Schrank, "*Triton alpestris*" Laurenti) in the same "Deutschlands Fauna".

2.3. An enormous increase of knowledge since 1800

Since about 1800 the knowledge in natural science increased immensely and many new species were described. Laurenti's (1768) system of splitting the Linnean genera began to win recognition. Nonetheless, Laurenti's total replacement of the generic name *Lacerta,* e.g. by *Seps*, was usually not accepted.

Some months after the issue of Sonnini & Latreille's (1801) encyclopaedia Daudin started his "Histoire Naturelle des Reptiles" ("An X" = 1801; see Harper 1940 for the exact data). His "Second ordre. Les Reptiles Sauriens" approximately conforms with the genus *Lacerta* lumped by Linnaeus and Lacepède (1789), but the salamanders were transferred to his fourth order "Les Reptiles Batraciens" comprising also the frogs. His genus *Lacerta* is one of 16 genera within these "sauriens", most of them being current lacertids except the Ameivas. His generic systematics resembles Laurenti's (1768) splitting system in general. One of the decisive differences was its essential feature in the formal persistence of a large genus *Lacerta*, whereas Laurenti's generic name *Seps* was made use of for only some two- or four-legged saurians. Daudin's greatest progress may be the redivision of his newly split genus *Lacerta*: It comprised 32 species subdivided into seven unnamed "sections". These sections presage the present lacertid genera in some very ambiguous outlines. For example, his second section "Lézards verds" contains *Lacerta ocellata* (now *Timon lepidus*) and *Lacerta viridis* (now: within *Lacerta* s. str.) as well, whereas his fourth section "Lézards tachetés" contains "*Lacerta lepida"* (a young *Timon lepidus*) and his new *Lacerta maculata* (a very cryptic name in some respects). Especially with Daudin the level of knowledge began to increase immensely. This growth did not only include further generic taxa but also an inflation of species names by naming "real" new species, also individual or local variations, both sexes or juveniles. Replacement names took the upperhand more and more. The names for the one current species *Lacerta agilis* (three *Seps* species names in Laurenti (1768); see Schmidtler 2004 and Kuzmin 2005) were augmented by Daudin to three more names (male, female, young) in his fifth section "Lézards gris". This fifth section comprised also his "lézard gris" with the Latin name "*Lacerta agilis*" (currently *Podarcis muralis*).

Until very recently Oppel (1811, see Fig. 16) was held as the author of the family Lacertidae ("Lacertini") (now: Lacertidae Batsch, 1788; cf. e.g. Speybroeck & al. 2010). Based upon Duméril (1806) he moved ahead the systematics in the higher categories and made them clear by trees as a forerunner of evolutionary ideas (Schmidtler 2009).

Merrem (1820) was the first to publish a schematic image and a terminology of the lacertid head scutellation (chapter 3, Fig.12). His genus *Lacerta* comprised 27 species, some of them being new. His systematics is based in general upon Daudin (1801–1803), Oppel (1811) and Cuvier (1819). He introduced some new terms and taxa in the higher categories. So his genus *Lacerta* is part of the "stirpes" A. Ascalabotae, the "tribus" 1. Gradientia, the III. order Squamata and the class 1. Pholidota (the 2. class is named Batrachia).

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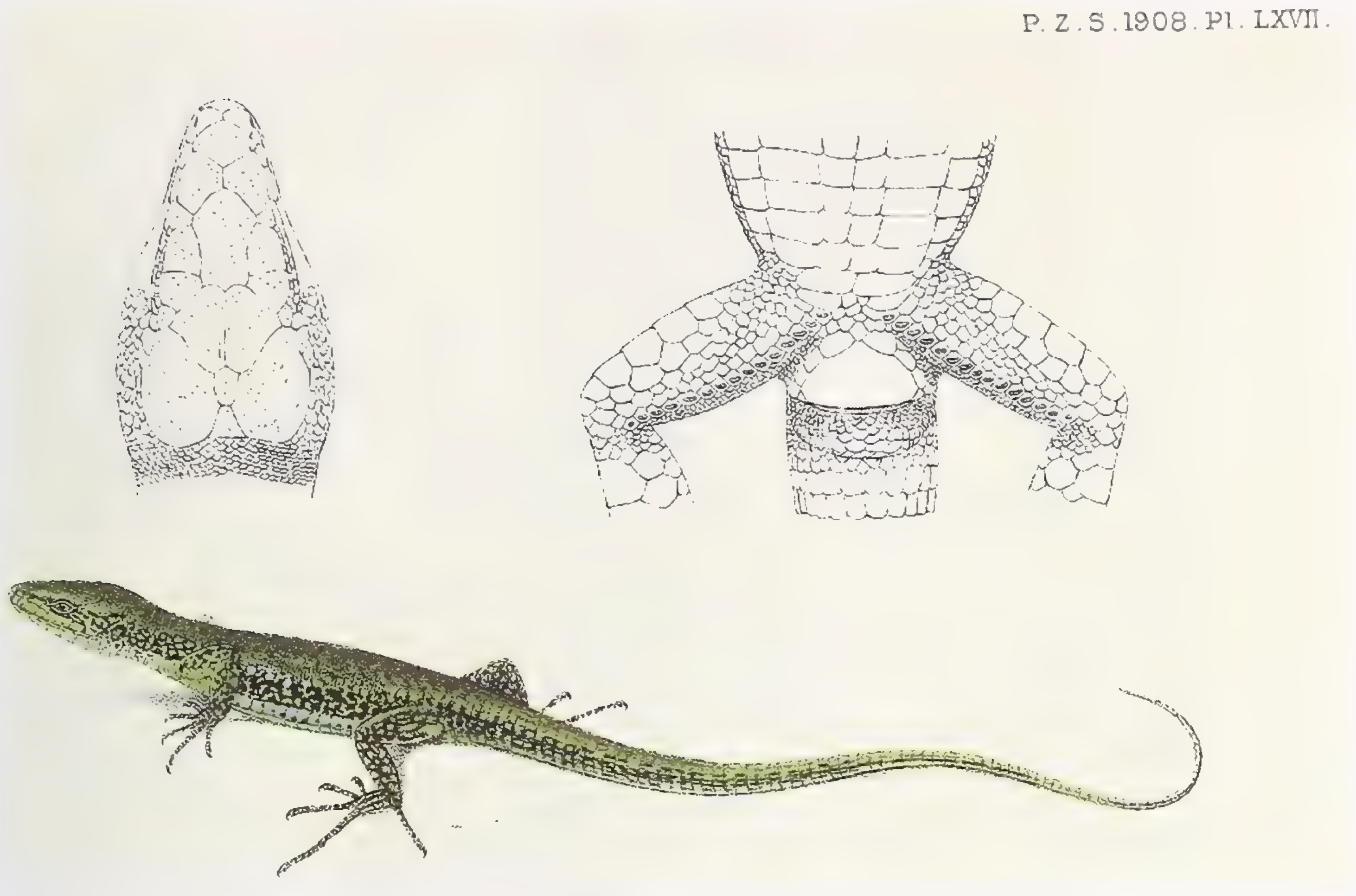

P. Z. S. 1908. Pl. LXVII.

Fig. 8. *Lacerta chlorogaster (= Darevskia chlorogaster)* from Boulenger (1909: Pl. LVII). Below one chromolithograph (i.e. an image printed successively with differently coloured lithograph plates), and above two (pen-) lithographs (scutellation of pileus and surroundings of the anal region). The highly informative combination of naturalistic and schematic figures upon one lithographic plate turned up at first in the middle of the 19th century.

The "Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften" was Fitzinger's (1826) first important work (see Mertens, 1973). His "XI. Familia. Lacertoidea. Lacertoiden" comprises three genera, among them *Lacerta* with 17 species. It was apparently the first time in a systematic listing that neither this family nor the genus *Lacerta* comprehended any taxa now being ranked outside the present-day Lacertidae.

It was the age of the great systematic monographs and shortly afterwards Wagler (1830) published his "Natürliches System der Amphibien mit vorausgehender Classification der Säugethiere und Vögel". Wagler's monograph is especially distinguished by comprehensive and progressive morphological and anatomical descriptions and considerations (pp. 211–344). His genus *Lacerta* only comprised lizards belonging to the current genera *Lacerta* (s.str.) and *Timon*. His "Familia III. L. autarchoglossae" comprehended the Linnean taxa *Lacerta* and *Tachydromus*, as well as the new lacertid genera *Zootoca, Podarcis, Aspistis, Psammuros* (the latter two are still synonyms of *Psammodromus* Fitzinger), apart from some genera belonging to other current families. *Zootoca* and *Podarcis* were regarded mostly as synonyms subsequently, but were revalidated more than 150 years later. All in all Wagler's systematics of the genus *Lacerta* appears rather modern (Fig. 1).

The "Histoire Naturelle des Reptiles" in eight large volumes by Duméril & Bibron (1834–1854) represents a new kind of herpetological monograph, compared with Daudin's (1801–1803) work. Especially because of the immense growth of knowledge the different species chapters increased, comprising different sub-chapters (e.g. in *Lacerta vivipara*: "caractères, synonymie, déscription" with "patrie et moeurs" in seven pages). His species chapters on *Lacerta* were based on many detailed new works, including also relatively new disciplines (e.g. reproduction biology) by Milne Edwards (1829), Dugès (1835), Cocteau (1835) and Tschudi (1837). Duméril & Bibron (1839) were lumpers, compared with Wagler (1830). Their genus *Lacerta* comprised 16 species (some of them new), subdivided into three species groups. Their genus *Lacerta* is currently ranked in 14 genera, some of them having

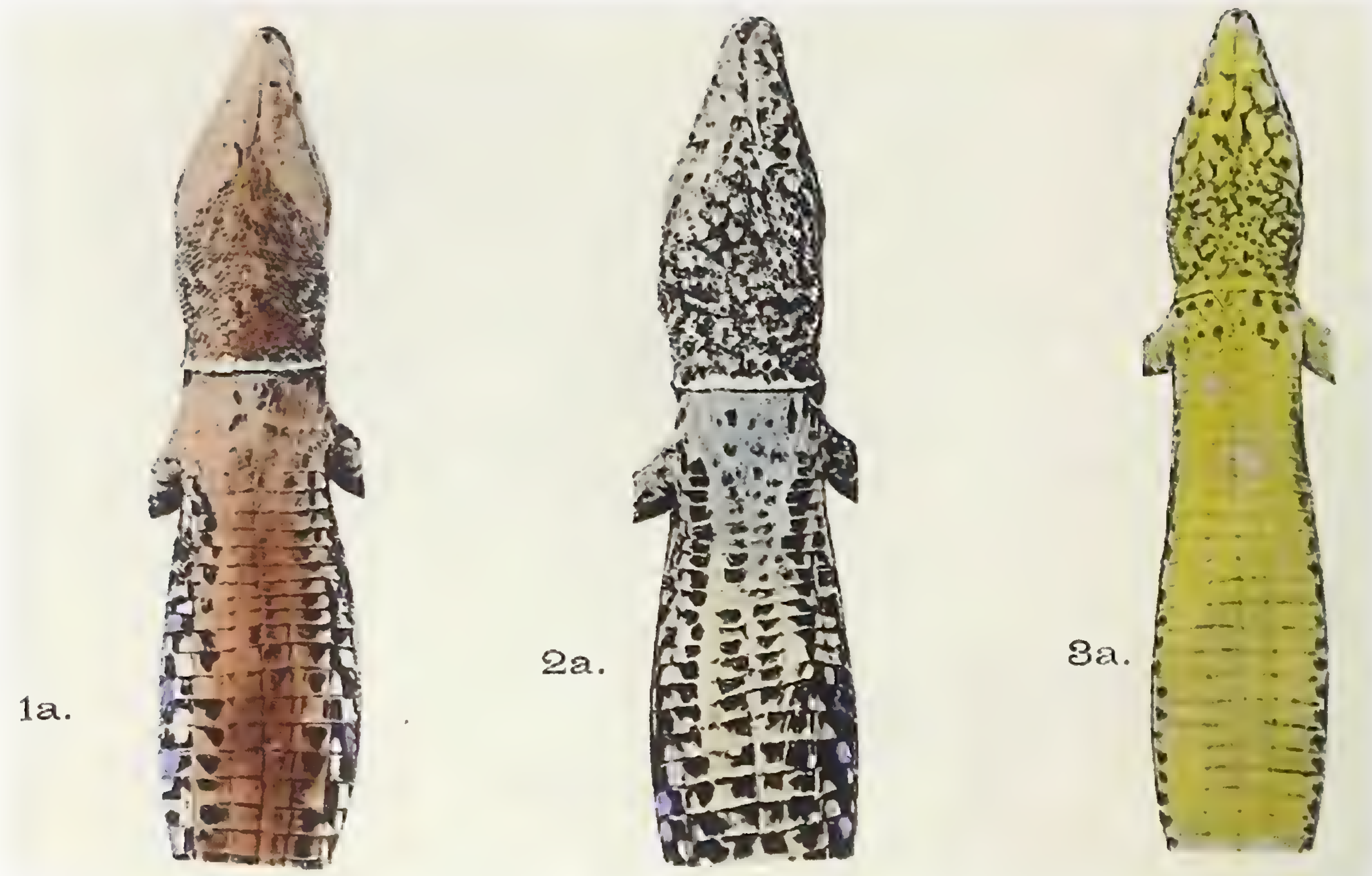
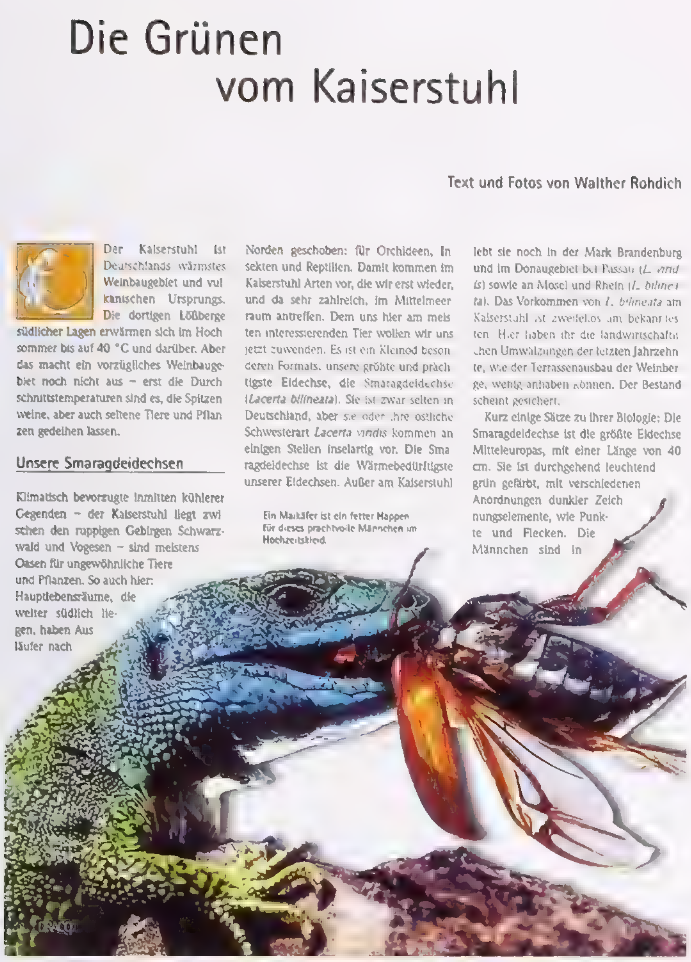


Fig. 9. Ventral sides of "*Lacerta muralis* vars. *lilfordi / serpa / brueggemanni"* (i.e. now three different species of *Podarcis*), from Boulenger (1905: pl. XXII). – Hand coloured photos (The combination of hand colouring and photographs was very unusual then in natural science). The spotting and the colouration are of systematic importance in these "varieties". The diagnostic features, especially the sutures of the shields, are not presentable simultaneously in the same figure (See Fig. 8!). – In 1853 the new technique of photography had been received with enthusiasm after a publication on reptiles (varans and a crocodile) and other animals ("Even the best painter would not have the patience and ability to make visible all the details and structures…"; see Niekisch 2010).

been described before Duméril & Bibron. The present-day Lacertidae corresponds to Duméril & Bibron's subfamily "Coelodontes" comprising nine genera. Duméril & Bibron (1839: 1–19; 181–189) published a substantial historical outline of their family "Lacertiens ou Autosaures" and their genus *Lacerta,* respectively.

It is worth mentioning the chapters on "Erpétologie" or "Lézards" in different French natural science dictionaries, which are now more or less forgotten. They mirror imposingly the general advances in herpetology between 1800 and 1850 and in *Lacerta* in particular: See Bosc d'Antic (1817: 521–528), Cloquet (1819/1823), Bory de Saint-Vincent (1826/1828), Cocteau (1835) and Meunier in Guérin (1836).

Contrary to Duméril & Bibron (1839), Fitzinger (1843) proved to be a splitter. Within his class Reptilia he included the categories "Series", "Ordo", "Tribus" and "Familia". The present-day Lacertidae were divided into three families: Lacertae, Tachyscelides and Eremiae. His first family Lacertae comprised four genera (*Scelarcis, Podarcis, Chrysolamprus, Lacerta*), most of them being subdivided into subgenera. As Mertens (1973: V) stated, Fitzinger's (1843) work is of tremendous significance for the study of amphibians and reptiles, not so much of the nearly one hundred new generic and subgeneric names proposed, but because he always cited generic type species. In the case of *Lacerta* this tremendous significance is manifested in Fitzinger's (1843: 20) determination of "*Lacerta agilis*. Linné" as the type species of *Lacerta.* The excellent coloured engraving by Wolf (1799) may have been here the decisive motive. Like Kaup (1836; see also Fig. 17), Fitzinger (1843: 12) was also a follower of the so called, unusual "Naturphilosophie" (natural philosophy), then distributed above all among German speaking natural scientists.



Die Grünen vom Kaiserstuhl

Text und Fotos von Walther Rohdich

Der Kaiserstuhl ist Deutschlands wärmstes Weinbaugebiet und vulkanischen Ursprungs. Die dortigen Lößberge südlicher Lagen erwärmen sich im Hochsommer bis auf 40 °C und darüber. Aber das macht ein vorzügliches Weinbaugebiet noch nicht aus – erst die Durchschnittstemperaturen sind es, die Spitzenweine, aber auch seltene Tiere und Pflanzen gedeihen lassen.

Unsere Smaragdeidechsen

Klimatisch bevorzugte inmitten kühlerer Gegenden – der Kaiserstuhl liegt zwischen den ruppigen Gebingen Schwarzwald und Vogesen – sind meistens Oasen für ungewöhnliche Tiere und Pflanzen. So auch hier: Hauptlebensräume, die weiter südlich liegen, haben Ausläufer nach Norden geschoben: für Orchideen, Insekten und Reptilien. Damit kommen im Kaiserstuhl Arten vor, die wir erst wieder, und da sehr zahlreich, im Mittelmeerraum antreffen. Dem uns hier am meisten interessierenden Tier wollen wir uns jetzt zuwenden. Es ist ein Kleinod besonderen Formats, unsere größte und prächtigste Eidechse, die Smaragdeidechse (*Lacerta bilineata*). Sie ist zwar selten in Deutschland, aber sie oder ihre östliche Schwesterart *Lacerta viridis* kommen an einigen Stellen inselartig vor. Die Smaragdeidechse ist die Wärmebedürftigste unserer Eidechsen. Außer am Kaiserstuhl lebt sie noch in der Mark Brandenburg und im Donaugebiet bei Passau (*L. viridis*) sowie an Mosel und Rhein (*L. bilineata*). Das Vorkommen von *L. bilineata* am Kaiserstuhl ist zweifelos am bekanntesten. Hier haben ihr die landwirtschaftlichen Umwälzungen der letzten Jahrzehnte, wie der Terrassenausbau der Weinberge, wenig anhaben können. Der Bestand scheint gesichert.

Kurz einige Sätze zu ihrer Biologie: Die Smaragdeidechse ist die größte Eidechse Mitteleuropas, mit einer Länge von 40 cm. Sie ist durchgehend leuchtend grün gefärbt, mit verschiedenen Anordnungen dunkler Zeichnungselemente, wie Punkte und Flecken. Die Männchen sind in

Ein Maikäfer ist ein fetter Happen für dieses prachtvolle Männchen im Hochzeitskleid.

Fig. 10. Male of *Lacerta bilineata* from the journal "Reptilia" (Nr. 20, 2004: 68): A perfect layout and a perfect digital colour photo have been combined here. The beautiful and viewable photos serve firstly for keepers (demonstrating feeding habits, etc.) and field herpetologists (identification in the field / shop) in popular articles. In the light of modern genetic methods the images have lost their traditional predominance in underlining systematic descriptions.

2.4 The era of George Albert Boulenger (ca. 1880–1920)

The end of the 19th century was initially characterised by new questions and topics as is displayed by Eimer's (1881) indication of «darwinism» in the caption of his article. There infrageneric and infraspecific, geographical researches came to the fore. I should like to emphasize the basic advances, such as his formation of terminologies in the dorsal pattern (Fig. 14). We may remember here his long-standing controversy with Bedriaga concerning the origin of colouration in insular lizards (see Müller 1994).

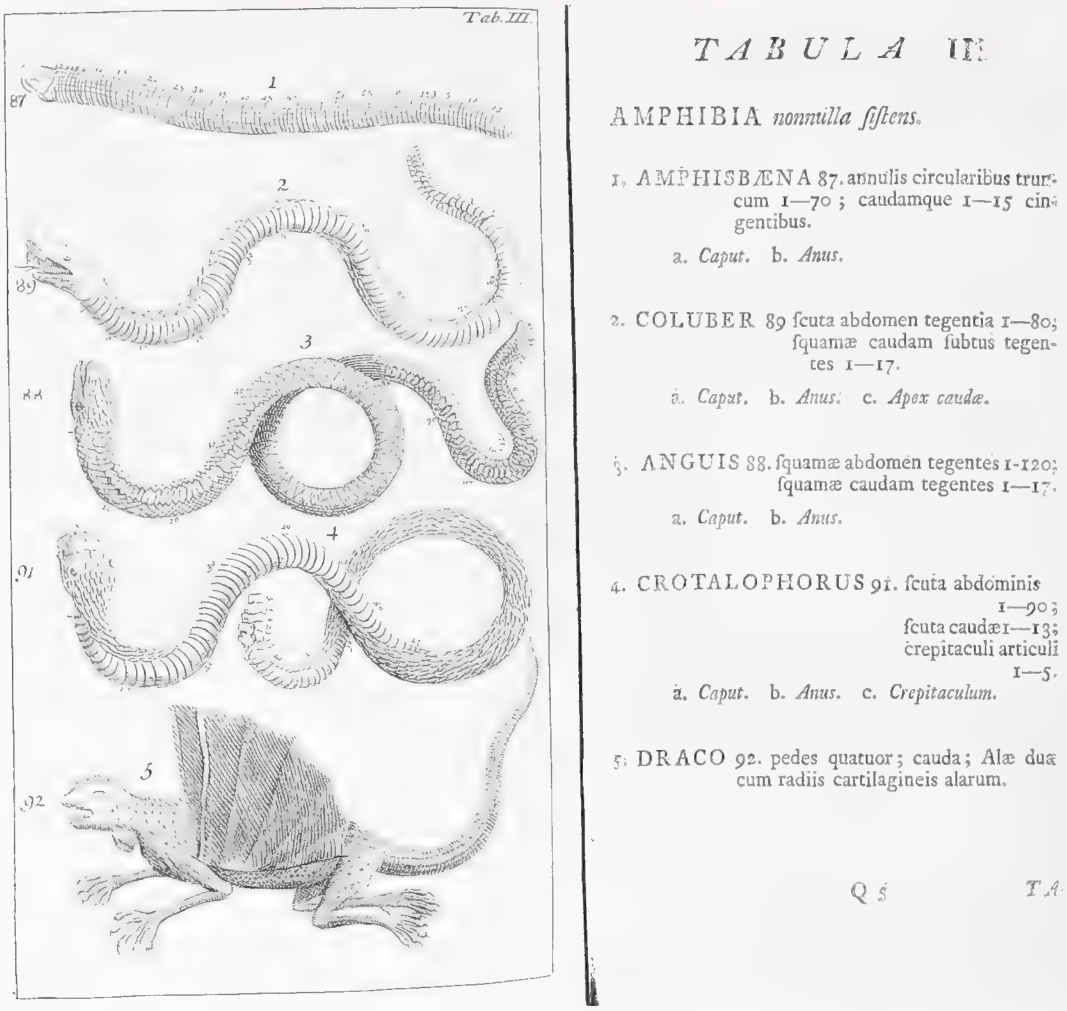
In this Darwinian sense Bedriaga (1886) tried to explain the phylogenetic relations and origins of lacertid taxa (the genus *Lacerta* with the five subgenera *Lacerta, Algyroides, Tropidosaura, Zerzumia, Bettaia*) by detailed discussions. His subgenus *Lacerta*, however, contained still species of all current subfamilies and tribes. With respect to book illustration (see chapter 3) it may be regretted that his descriptions were corroborated by a single lithographic plate only. The reasons here – as ever – may have been economical ones.

Simultaneously the time of Boulenger's great comprehensive catalogues in herpetology commenced. In the introduction of his Catalogue of the Lizards (three volumes) Boulenger (1887) displayed the immense increase in the numbers of lacertid species known and characterized: Duméril & Bibron (1839), 43 species – Gray (1845), 57 species – Boulenger (1887), 97 species. Boulenger's Lacertidae comprised 17 genera and his genus Lacerta comprised 21 species, among them species of the whole Eurasian and African range, i.e. species within the current subfamilies Gallotiinae and Lacertinae (some species of the current tribe Eremiadini not excluded; see Figs 1 and 19). The chapter «11 *Lacerta muralis*» (1887: 28) with many «varieties» underlines his very typical species concept. Boulenger's vol. III contains a set of excellent lithographs, among them the new species *L. parva* (now *Parvilacerta*) and *L. yayakari* (now *Omanosaura*).

Méhely (1909) carried out intensive studies on morphology and osteology of European and Caucasian lacertids. Aside from the further development of the terminology of scutellation, osteology (Fig. 13), and pattern of muralis-like lacertids, he described the genus *Apathya* and the «I. Gruppe: Archaeolacertae» of his genus *Lacerta*, comprising species of the current genera *Anatololacerta, Phoenicolacerta, Hellenolacerta, Dinarolacerta, Iberolacerta* and *Darevskia*. His victorious species concept («species» instead of Boulenger's *L. muralis*-varieties) displays his famous controversy with Boulenger.

Schreiber (1912) adopted the view of Méhely and his species concept within the European-Caucasian lacertids. Within the current genus *Podarcis* he accepted as the first in a large monograph not less than eight species, most of them, especially *Lacerta muralis* and *Lacerta serpa (= Podarcis siculus)*, comprising many varieties and subvarieties.

Boulenger (1920 / 1921), covered the lacertids in their whole Eurasian and African range. Irrespective of the acceptance of six «sections» within *Lacerta* he insisted upon his system of the one *muralis*-like species, following his catalogue (Boulenger, 1887) and later papers (1905 and 1913 especially; see Fig. 19). His *Lacerta muralis* (belonging to his subgenus *Podarcis* Wagler) covers not less than 31 (!) «varieties». Most of them are presently species or subspecies or invalid forms within the genus *Podarcis*, but there are also taxa of the current genera *Archaeolacerta, Iberolacerta* and *Darevskia* to be found. It seems now that



TABULA III.

AMPHIBIA *nonnulla ſiſtens.*

1. AMPHISBÆNA 87. annulis circularibus truncum 1—70; caudamque 1—15 cingentibus.
a. *Caput.* b. *Anus.*

2. COLUBER 89 ſcuta abdomen tegentia 1—80; ſquamæ caudam ſubtus tegentes 1—17.
a. *Caput.* b. *Anus.* c. *Apex caudæ.*

3. ANGUIS 88. ſquamæ abdomen tegentes 1-120; ſquamæ caudam tegentes 1—17.
a. *Caput.* b. *Anus.*

4. CROTALOPHORUS 91. ſcuta abdominis 1—90; ſcuta caudæ 1—13; crepitaculi articuli 1—5.
a. *Caput.* b. *Anus.* c. *Crepitaculum.*

5. DRACO 92. pedes quatuor; cauda; Alæ duæ cum radiis cartilagineis alarum.

Q 5 TA-

Fig. 11. Some reptiles and their scale countings depicted by Linnaeus (1756: Tab. III; 9th edition. Copper engraving). The scale countings refer mostly to the ventrals and subcaudals in snakes and were given especially in the text on the genus *Coluber*. In the diagnoses of the genus *Lacerta* no scutellation features were used then. This is apparently the first attempt of a schematic delineation and description of body shields in herpetology. The same features were used also, without depictions, in the text of the 10th and 12th editions (1758 / 1766).

his system was a relatively superficial morphological one, because he accepted also some (morphologically) conspicuously different species besides his «*L. muralis*», like *Lacerta taurica* (now within *Podarcis*), or *Lacerta chlorogaster* (now within *Darevskia*). This was one of Boulenger's rare mistakes in which, soon later, the herpetologists of this time did not follow his exceptional authority.

Mertens & Müller (1928) adopted Boulenger's (1920) European subgenera (*Archaeolacerta, Podarcis, Zootoca, Lacerta*), but they did not diverge in substance from the species concept of Méhely (1909) and Schreiber (1912). They were the first to accept geographical subspecies (see Wermuth in Böhme 1981), i.e. a trinominal nomenclature in European herpetology (e.g. «*Lacerta agilis exigua* Eichwald»). In addition they carried out some changes being nomenclaturally necessary (e.g. *Lacerta lepida* Daudin, 1802 - instead of the preoccupied *Lacerta ocellata* Daudin, 1802).

In Mertens & Wermuth (1960) there are considered many new discoveries of the European herpetofauna (especially new descriptions of many lizard subspecies of «*Lacerta*» *sicula, L. erhardii, L. melisellensis, L. lilfordi*, etc., from Mediterranean islands, by Cyrén, Müller, Wettstein, Radovanovic, Eisentraut, Buchholz, in various papers each, since the second list of Mertens & Müller (1940). Nevertheless this «Dritte Liste» characterizes the relatively stable generic and specific systematics and nomenclature in lizards between 1940 and 1990.

2.5 Towards a final breaking up of the genus Lacerta by new methods and techniques

The basic works of Arnold (1973, 1989) and Böhme (1971) broke new ground in the systematics of the Lacertidae. New techniques (genital-morphological, karyological, electrophoretical, albumin-immunological, genetic features) and modern univariate and multivariate statistics were executed.

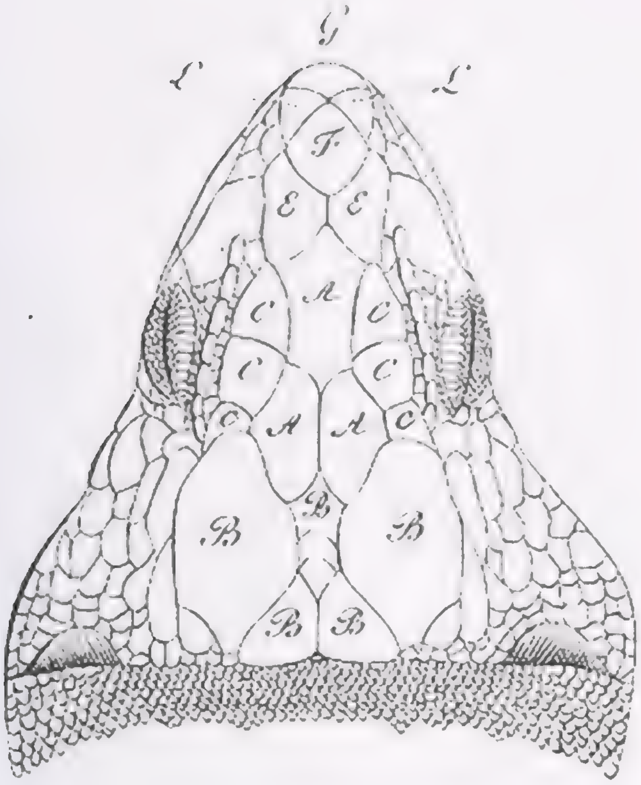


Fig. 12. Schema of the pileus scutellation in Merrem (1820: p. XII–XIII and fig. p. 191 upper part). (Pen-) lithography. – The decisive step ahead in the schematic depiction of lizards was made by Merrem (1820). Based upon his similar system in snakes (Merrem 1790 and 1820), he gave names to the pileus shields of an adult *Lacerta ocellata* (now: *Timon lepidus*; see his pages XII and XIII) and depicted their abbreviations in this figure. The description covered seven types of scutes with the letters A (Wirbelschilder – Scuta vertebralia), B (Hinterhauptschilder – Scuta occipitalia), C (Augenbrauenschilder – Scuta superciliaria), E (Stirnschilder – Scuta frontalia posterioria), F (Schnautzenschilder – Scuta frontalia anterioria), G (Rüsselschild – Scutum rostrale, L (Nasenlöcherschilder – Scuta nasalia). This system was later on differentiated and improved by Milne Edwards (1829: pls. 5–8) who depicted and described also the shields of the lower sides of head, body and limbs. The concept of Merrem (1820) and Milne Edwards (1829) remain valid today.

The first results of Arnold's (1973, 1989; see Fig.1) elaborate researches, based mainly on morphology were the revalidation of the old Waglerian genus *Podarcis* and of *Gallotia* Boulenger, 1916 (then a subgenus) besides two very preliminary groups, named "*Lacerta* groups I and II".

The taxonomic tentativeness at that time found its way into the comprehensive "Handbuch der Reptilien und Amphibien Europas" (Böhme in Böhme 1981, Böhme, 1981).

Mayer & Bischoff (1996) (re-) established further separations from the so far comprehensive genus *Lacerta* (*Zootoca, Omanosaura, Timon, Teira*). They visualized a phylogenetic tree of the Lacertidae from the relationships of their serum albumins.

The numerous and very detailed morphological works of Arribas (1997/1999) resulted in the splitting off of the mainly SW-European genus *Iberolacerta* Arribas 1997, and above all of the mainly Caucasian genus *Darevskia* Arribas, 1997 from *Lacerta*. Thereby also a very old controversy (especially of Méhely and Boulenger; see chapter 2.4) on the *muralis*-like "Archaeolacertae" could be finished. The name *Darevskia* was given in honour of the great Russian herpetologist I.S. Darevsky (1925–2009) who had detected parthenogenesis in these lizards, and therewith in reptiles (see Darevsky 1967; Schmidtler 2010).

Beginning with the comprehensive work of Harris et al. (1998) new genetic methods have also been adopted in the systematics of the lacertids and they have caused here, like everywhere in systematics, a revolutionary situation. DNA sequences from parts of the 12S, 16S and cytocrome b mitochondrial genes, together with morphological information, were used to estimate the relationships within the family. This work was continued by Arnold et al. (2007; Fig. 20 hoc loco). DNA sequences indicated that the Lac-

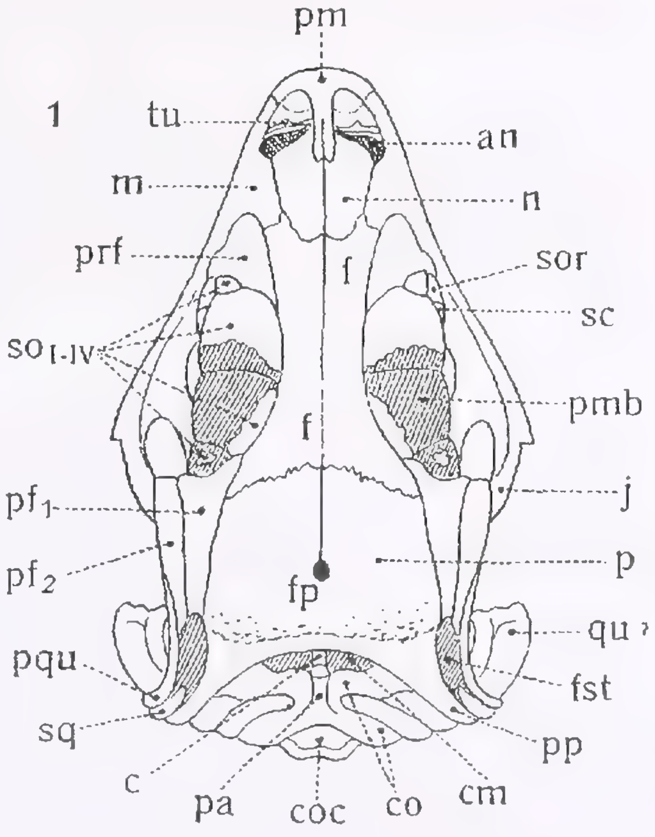


Fig. 13. Schema of skull bones (*"Lacerta horvathi"= Iberolacerta horvathi*) in Méhely (1909: Taf. X, upper part) on the basis of Siebenrock (1894). – In the middle of the 19th century important osteological investigations also were executed in lacertids. They allowed taxonomic research in the higher categories but also within lacertid genera and species, after a reasonable schematization in osteology, above all in skull terminology, had been found.

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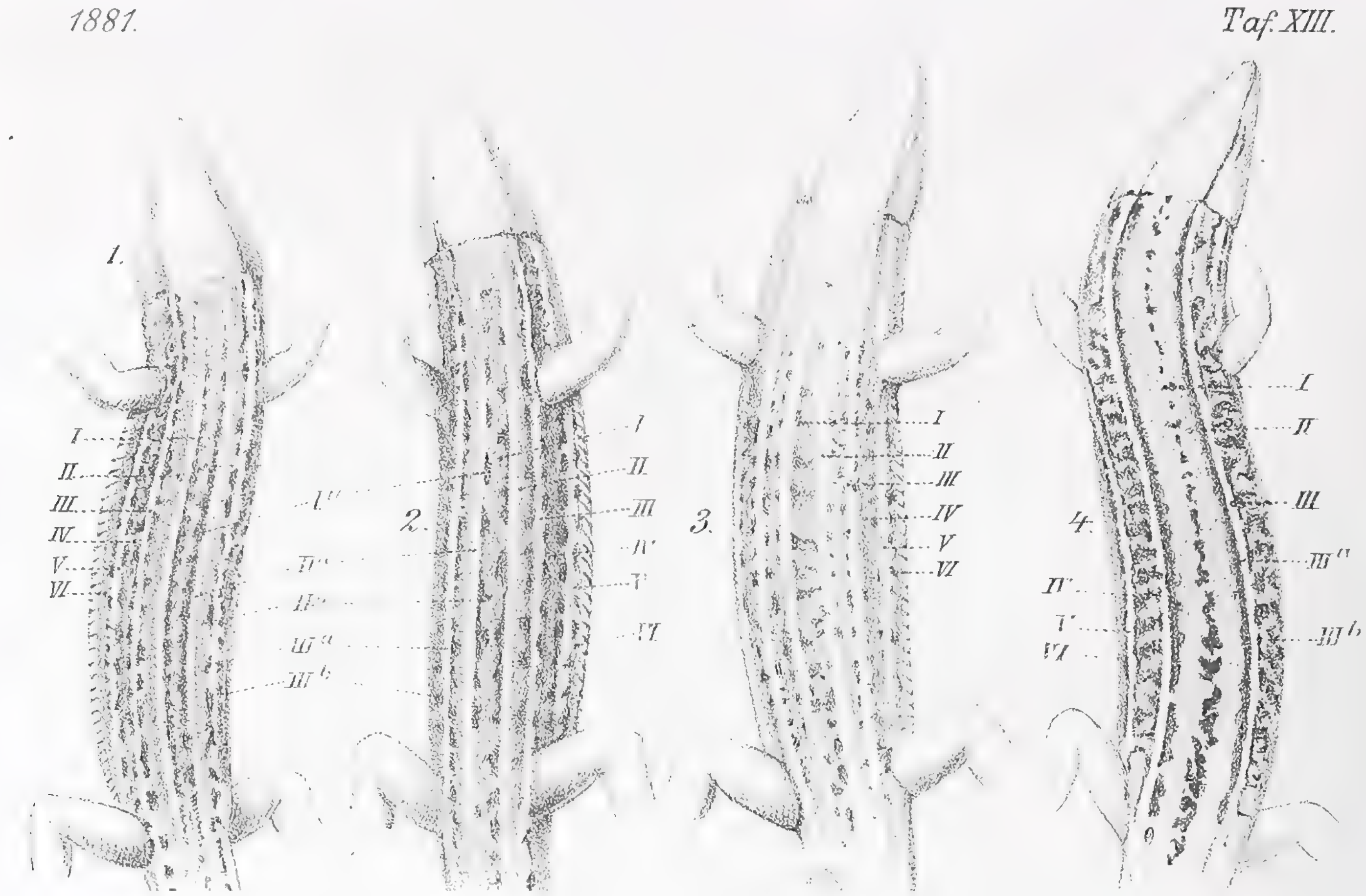

Fig. 14. Schema of the dorsal pattern in some *Podarcis* by Eimer (1881: Taf. XIII). Lithograph. It was the research since the middle of the 18th century which revealed the crucial importance of the dorsal pattern especially in the specific and infraspecific taxonomy of the current genus *Podarcis*. Eimer (1881: Taf. XIII) named the different longitudinal zones ("I bis VI erste bis sechste Zone") which usually exhibit a system of narrow light longitudinal streaks (nrs. I and III, "Grenzlinien") and dark bands (nrs. II," inneres / äußeres Band"). Méhely (1909: Fig. 1) eased his terminology and gave it the presently valid content; the seven light streaks and dark bands were named after their initial points at the pileus shields (like "Supraciliarstreifen" and "Occipitalband"); see also Schreiber (1912: Fig. 68; p. 333–335) and Mertens (1915: Fig. 3).

ertidae contain two subfamilies, Gallotiinae and Lacertinae, the latter comprising two monophyletic tribes, the Eremiadini of Africa and arid southwestern and central Asia, and the Lacertini of Europe, northwestern Africa and southwestern and eastern Asia. Relationships within the 108 species of Lacertini were explored using mtDNA for 59 nominal species. The morphology of the tribe was reviewed and also used to assess relationships. The Lacertini were assigned to 19 monophyletic units of 1 to 27 species. There were described five new Lacertini-genera out of the old collective genus *Lacerta*: *Dalmatolacerta, Dinarolacerta, Hellenolacerta, Iranolacerta, Phoenicolacerta* (see Fig. 20 for a complete listing of current genera). The new generic concept does not include subgenera except in *Iberolacerta* (*Pyrenesaura* Arribas, 1997). The genus *Lacerta* is presently restricted to eight species, the majority of them being polytypic: *Lacerta agilis* Linnaeus, 1758 (type species), *L. bilineata* Daudin, 1802, *L. media* Lantz & Cyrén, 1920, *L. pamphylica* Schmidtler, 1975, *L. schreiberi* Bedriaga, 1878, *L. strigata* Eichwald, 1831, *L. trilineata* Bedriaga, 1886, *L. viridis* Laurenti, 1768.

Thus the genus *Lacerta* appears to have finished its reduction through the centuries (Fig. 1) and to have stabilized at a level a little above the species level (according to the biological species concept). It seems however, that the species systematics of the eight species of *Lacerta* has not yet drawn to a close.

3. THE INTERACTION OF VERBAL DESCRIPTIONS AND ILLUSTRATIONS IN LACERTID TAXONOMY

3.1 General notes

Zoological publishing in a modern sense, and together with it, zoological book illustration, started at the end of the middle ages, at the beginning of the renaissance era in the 16th century (Nissen 1978: 113). They included above all Belon, Gessner, Rondelet and Aldrovandi – all of them physicians – who did no more than see their crucial challenge in lining up reports and opinions of ancient

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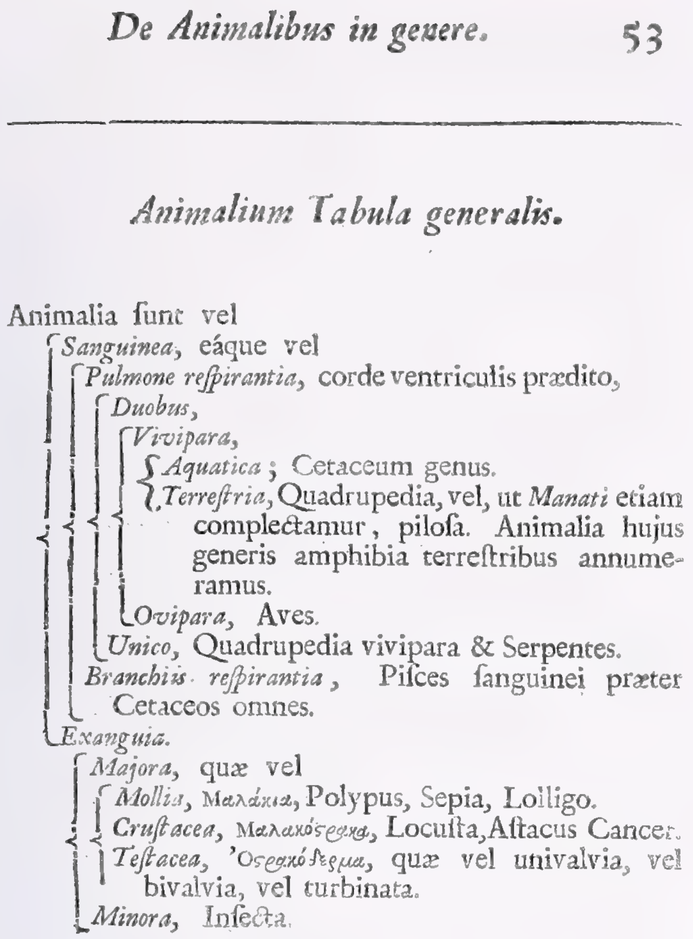


De Animalibus in genere. 53

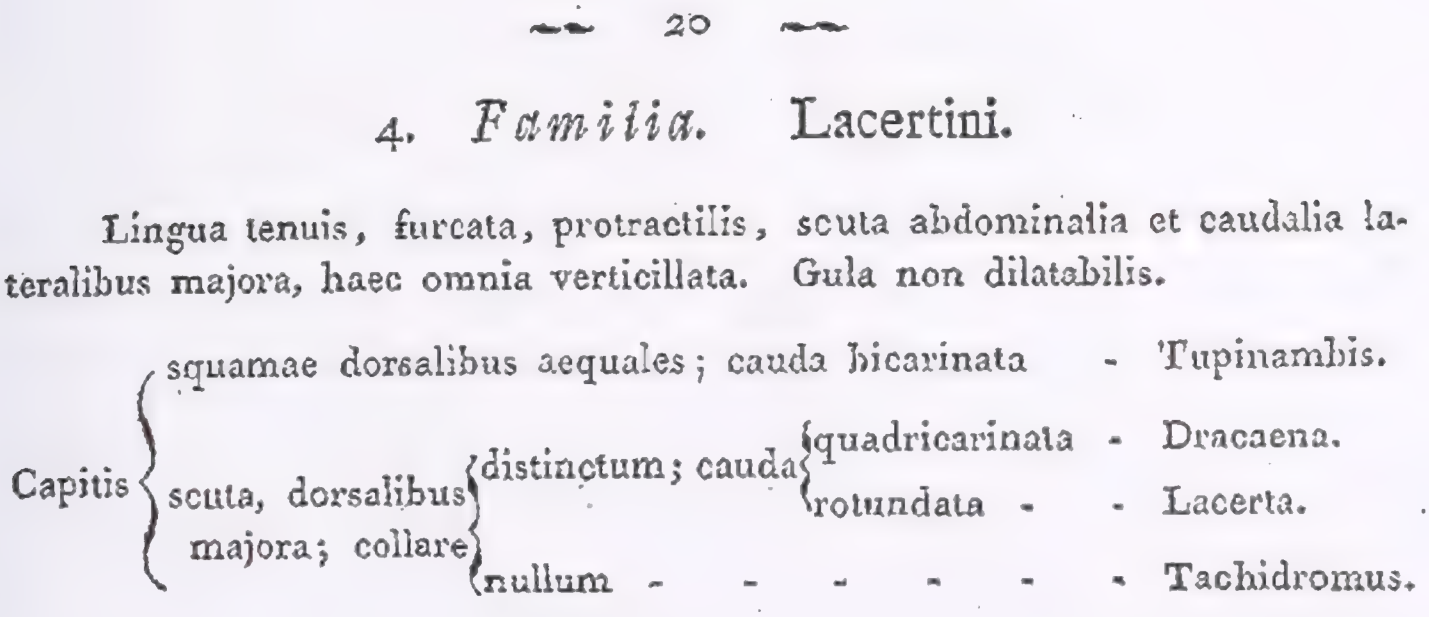
Animalium Tabula generalis.

Animalia ſunt vel
Sanguinea, eáque vel
Pulmone reſpirantia, corde ventriculis prædito,
Duobus,
Vivipara,
Aquatica; Cetaceum genus.
Terreſtria, Quadrupedia, vel, ut *Manati* etiam complectamur, piloſa. Animalia hujus generis amphibia terreſtribus annumeramus.
Ovipara, Aves.
Unico, Quadrupedia vivipara & Serpentes.
Branchiis reſpirantia, Piſces ſanguinei præter Cetaceos omnes.
Exanguia.
Majora, quæ vel
Mollia, Μαλάκια, Polypus, Sepia, Loligo.
Cruſtacea, Μαλακόστρακα, Locuſta, Aſtacus Cancer.
Teſtacea, Ὀστρακόδερμα, quæ vel univalvia, vel bivalvia, vel turbinata.
Minora, Inſecta.

Fig. 15. From Ray (1693): First attempt to exhibit affinities or relationships in animals by a tree-like diagram; comprising also amphibians and reptiles.

authors without criticism. They made rather use of these earlier authors descriptions to identify the indigenous fauna. They began to understand the pedagogic function of images and the importance of accuracy in representing the natural things in order to objectively describe them. The most important collection of natural history coloured paintings, among them 50 tables with amphibians and reptiles, originates from Ulisse Aldrovandi (1522–1605), having been detected for science and described in the last years. "Their number and quality allow this collection of images to be considered as the first attempt to organize an iconographic atlas of the Italian and Mediterranean fauna and, without any doubt, the first collection of herpetological images realized with relatively modern criteria" (Delfino, 2007; Delfino & Alessandro, 2008; Alessandrini & Ceregato, 2007). The lack of a species concept and the lack of the understanding of the animal organism, as well as the use of different engraving- and printing techniques (above all wood cuts) caused an excessive simplification in most contemporary publications and rendered the figures useless to represent the distinctive character of a species (cf. Gessner's figure; Fig. 2 hoc loco). The different insights of a painter and a mere engraver as well as the different qualities of a water colour and an engraving are shown by a comparison of an Aldrovandi water colour (Fig. 3).

It was about 250 years later, when the zoologist Hermann Schlegel (see Schmidtler, 2007) delved into the theory of natural science images (German translation in Nissen,



— 20 —

4. *Familia.* Lacertini.

Lingua tenuis, furcata, protractilis, scuta abdominalia et caudalia lateralibus majora, haec omnia verticillata. Gula non dilatabilis.

Capitis
squamae dorsalibus aequales; cauda bicarinata - Tupinambis.
scuta, dorsalibus majora; collare
distinctum; cauda
quadricarinata - Dracaena.
rotundata - - Lacerta.
nullum - - - - - - Tachidromus.

Fig. 16. Diagram of the family "Lacertini" in Oppel (1811): Oppel (1811: 20) established the family "Lacertini" (now: Lacertidae), among six families within his order "Squamata". The "Lacertini" comprised four genera, two of them (*Tupinambis* and *Dracaena*) belonging now to other families, before Duméril (1806: No. 49-51) had established two families only ("Planicaudati" and "Tereticaudati") in his order "Saurii".– Similar trees or identification keys like this and Duméril's were the forerunners of an evolutionary view in herpetology (see Schmidtler 2009).

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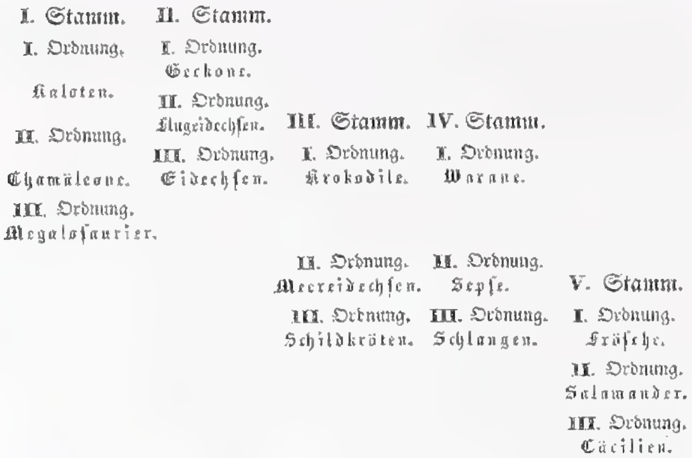
I. Stamm.
I. Ordnung.
Kaloten.
II. Ordnung.
Chamäleone.
III. Ordnung.
Megaloſaurier.
II. Stamm.
I. Ordnung.
Geckone.
II. Ordnung.
Flugeidechſen.
III. Ordnung.
Eidechſen.
III. Stamm.
I. Ordnung.
Krokodile.
II. Ordnung.
Meereidechſen.
III. Ordnung.
Schildkröten.
IV. Stamm.
I. Ordnung.
Warane.
II. Ordnung.
Sepſe.
III. Ordnung.
Schlangen.
V. Stamm.
I. Ordnung.
Fröſche.
II. Ordnung.
Salamander.
III. Ordnung.
Cäcilien.

Fig. 17. Diagram from Kaup (1836): His "III. Ordnung Eidechsen" („Lacertae", text p. 26) corresponds to the rank of the present day family Lacertidae, comprising several genera like the "eigentliche Eidechsen" = *Lacerta*. His "Stamm" corresponds nearly to a current order. In this diagram there is exhibited the famous and strange dead end of "natural philosophy"; displaying more a mysticism of numbers than a concept of natural science: Like in birds, mammals and amphibians as well, there exists in Kaup only a strict number of **five** "Stämme" and in each there are enclosed strictly **three** "Ordnungen"! See chapter 3.4. This mysticism does not proceed in the number of lacertid genera. See also Fitzinger (1843) and the critique in Mertens (1973).

1978: 231). According to him it is the function of such a figure to supersede the subjects difficult to be seen or examined in nature, in order to recognize them after the depiction and to be able to derive their shape, colours, proportions and other features as exact as possible. The perfection of this claim calls for a full interaction of text and illustration in the scientific, artistic and technical aspects – in this article being demonstrated on the basis of the Linnean genus *Lacerta.*

When the taxonomic importance of the different structures, like scales, spotting and colouration had been recognized about 1800, there originated also the need to display them separately from each other. The joint – naturalistic – appearance interfered with their independant perceptibility, for instance because of their poor visibility (e.g. sutures of scutes), overlapping with spotting, light reflection (Figs 8, 9), etc. At the same time abstracted figures (diagrams) were also used to exhibit relationships and / or identification keys, etc. (Figs 15–20).

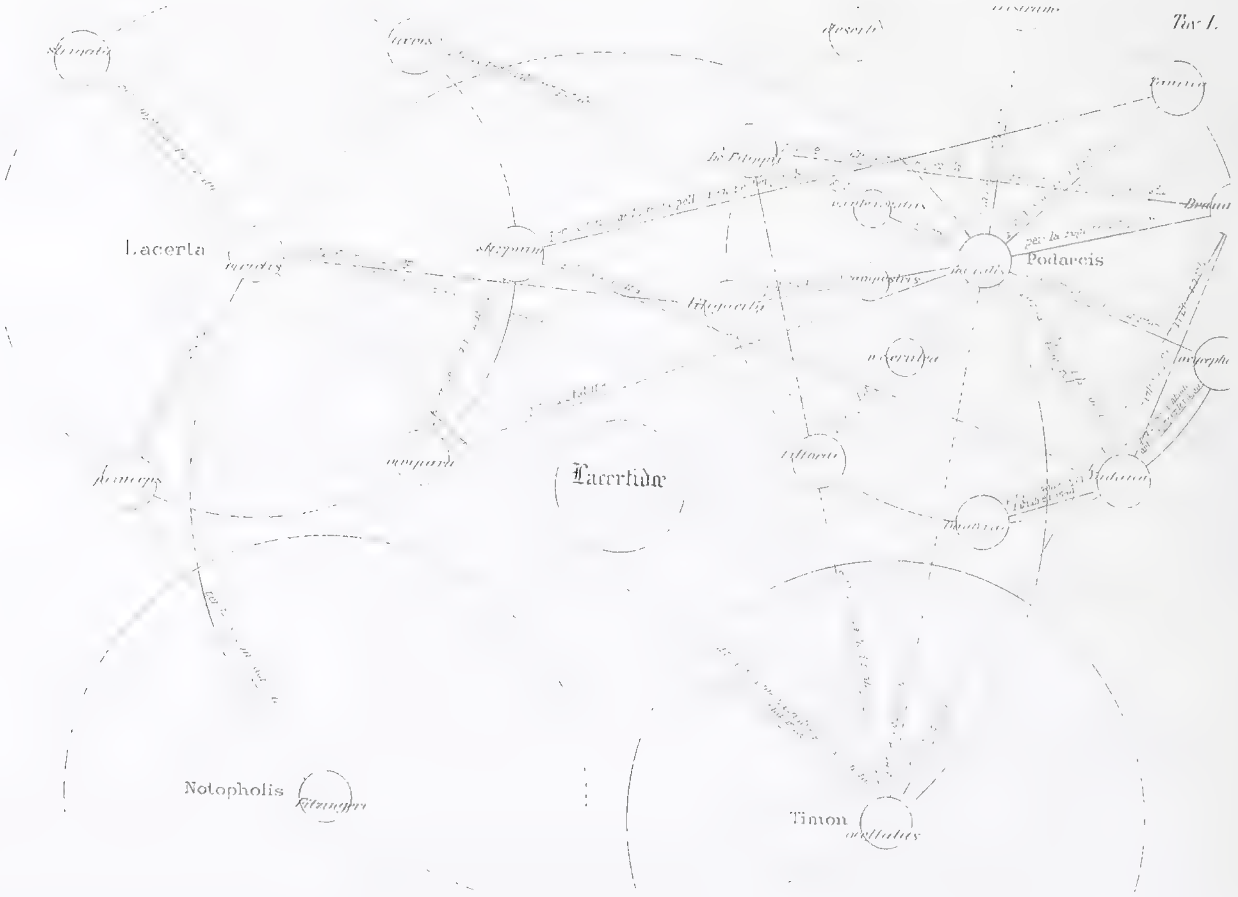
Tav. I.
Lacerta
Podarcis
Lacertidae
Notopholis
Timon

Fig. 18. From Camerano (1877: Tav. I, excerpt): Another rather popular kind of diagram displaying the relations between taxa. The small circles within the large circles symbolise related taxa of the four lacertid genera (*Lacerta, Podarcis, Notopholis, Timon*). The lines between such encircled taxa designate important morphological resemblances.

The first engraving – and printing – techniques were wood cuts (15th century), and shortly later, copper engravings. Around 1800 copper engraving was refined (etchings) and the first very expensive and rare colour prints in herpetology were based upon them (Daudin 1802; see Schmidtler 2007) after centuries of hand colouring. Lithography (the first lizards in Schmid 1819) was invented and improved more and more up to the time of chromolithography (see Fig. 8). Bewick (e.g. 1809–1816; Fig. 7) renewed the wood cuts ("Wood engraving"). In the second half of the 19th century the first photographs appeared (see Niekisch, 2010; Fig. 9 hoc loco) and revolutionised the book-illustration also in natural science and herpetology together with new letterpress printing techniques. These technical advances were attended by the expansion of some zoological / herpetological disciplines – or facilitated their proliferation – like ethology, husbandry, ecology.

It is noteworthy to emphasize that each of the engraving- and printing techniques displays its technical, artistic and economical strengths and weaknesses as measured by the different requirements they have to satisfy (see Schmidtler, 2007). Book illustrations were always expensive and this was the most important reason why the informative value of many important works had to suffer immensely.

3.2 Naturalistic figures

As was explained above, the lack of species recognition was especially responsible for rendering many figures useless in representing distinctive characters. This was especially the case for many of the reptiles, being regarded as abhorrent or less important (except the venomous snakes), compared to mammals or birds – up to the Linnean times and later.

A good example is Gessner`s fabulous creature (Fig. 1), called "*Lacertus viridis*", and typically attended with a poem advertising a medical and cosmetic prescription. It is only the indentations across the tail which suggests the possible belonging to the current Lacertidae.

Shortly before Linnaeus, the "Thesaurus" of the wealthy pharmacist Seba (1735) described many exotic animals from Seba's "Wunderkammer". This voluminous work depicted also many mythical creatures – besides some indigenous reptiles, e.g. the male of a "*Lacerta viridis*" (= *Lacerta agilis*), being identifiable only by means of the distinctive dorsal pattern and the green and brown colours (see Schmidtler, 2004: Abb. 1).

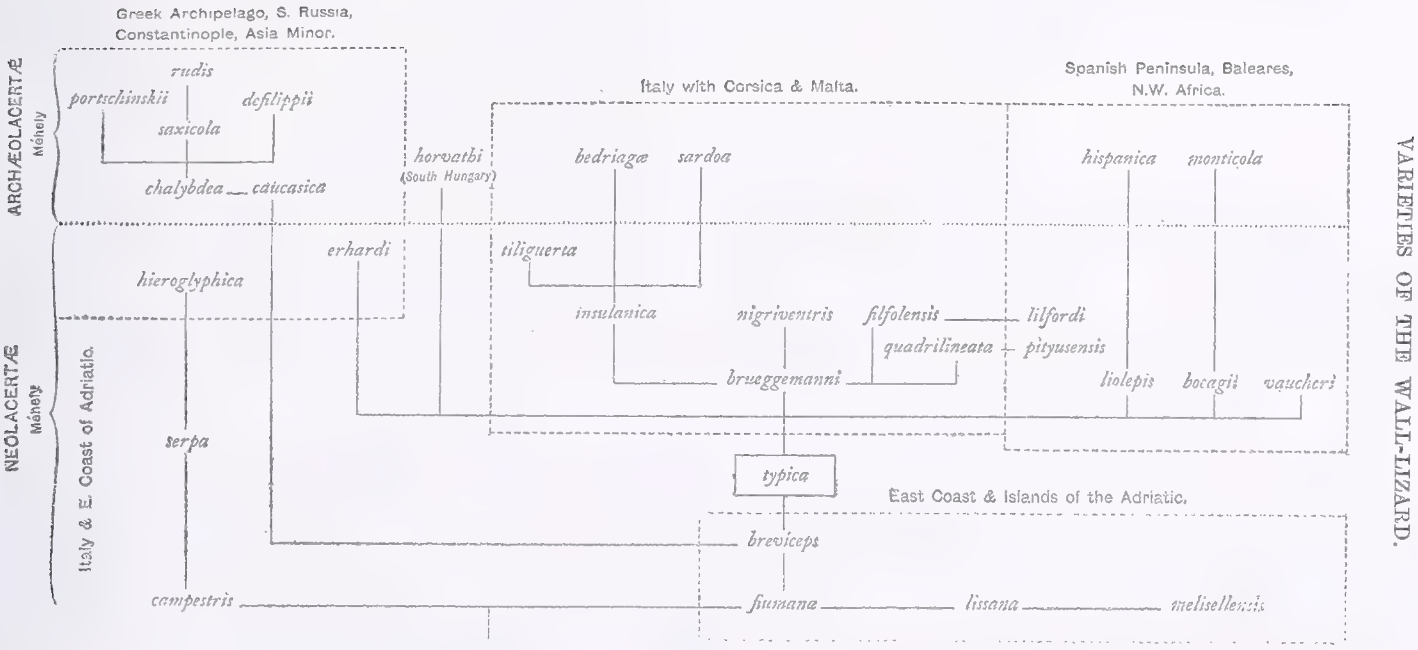
Greek Archipelago, S. Russia, Constantinople, Asia Minor.
ARCHÆOLACERTÆ
Méhely
rudis
portschinskii
defilippii
saxicola
chalybdea
caucasica
horvathi
(South Hungary)
Italy with Corsica & Malta.
bedriagæ
sardoa
Spanish Peninsula, Baleares, N.W. Africa.
hispanica
monticola
VARIETIES OF THE WALL-LIZARD.
erhardi
tiliguerta
hieroglyphica
insulanica
nigriventris
filfolensis
lilfordi
quadrilineata
pityusensis
brueggemanni
liolepis
bocagii
vaucheri
NEOLACERTÆ
Méhely
Italy & E. Coast of Adriatic.
serpa
typica
East Coast & Islands of the Adriatic.
breviceps
campestris
fiumana
lissana
melisellensis

Fig. 19. From Boulenger (1913: 205–206): Linear diagram of the forms of *Lacerta muralis*: Citation: "The preceding diagram expresses their affinities, as I conceive them, and also their distribution. It will also enable the reader to see at a glance how my views on the possible derivation of these forms differ from those advocated by Prof. Méhely." The "varieties" of Boulenger's only species "*Lacerta muralis*" comprise four current genera (*Podarcis, Darevskia, Iberolacerta, Archaeolacerta*) with at least 17 current species and some more subspecies.

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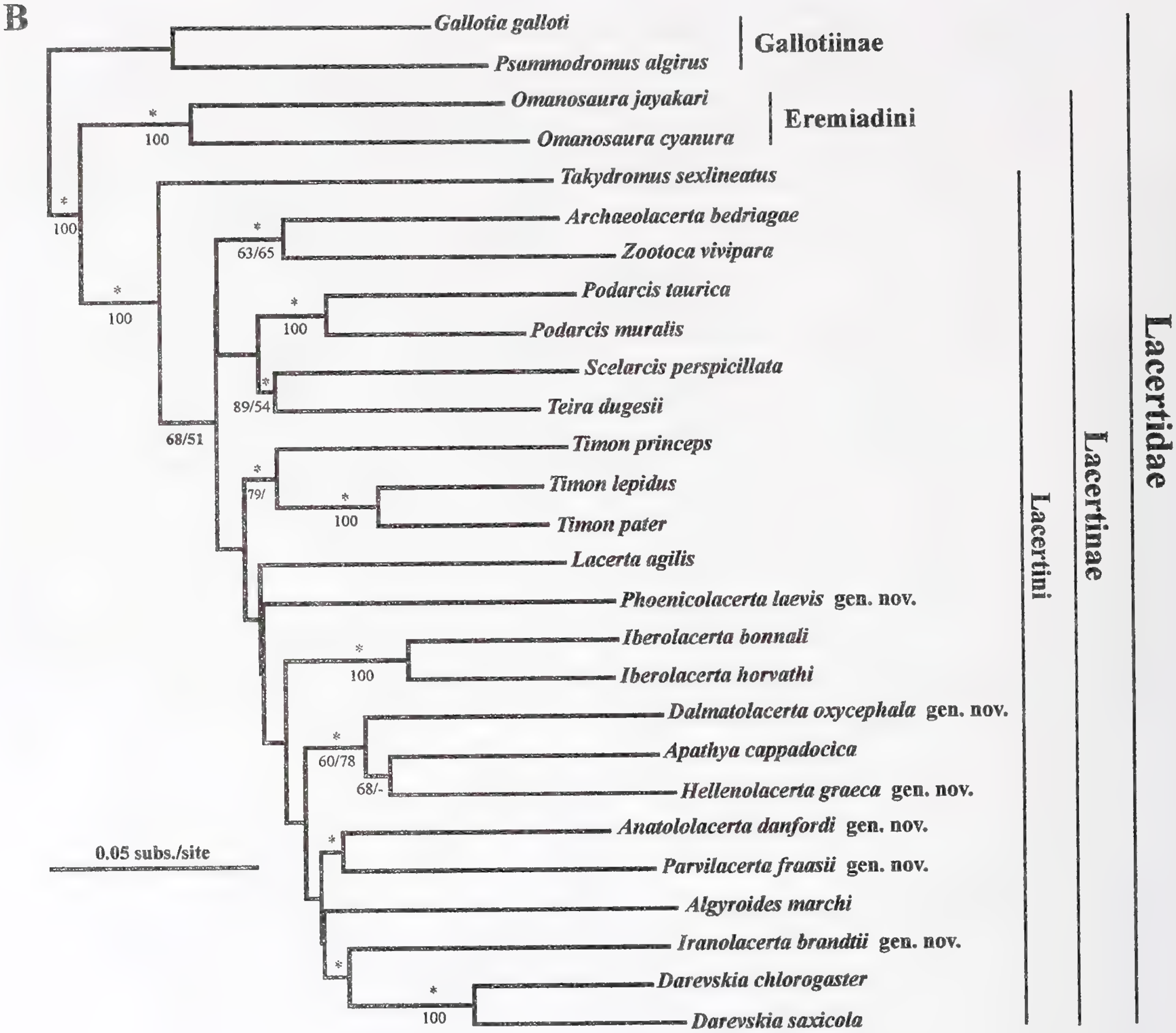
B
Gallotia galloti
Psammodromus algirus
Gallotiinae
Omanosaura jayakari
*
100
Omanosaura cyanura
Eremiadini
Takydromus sexlineatus
*
100
Archaeolacerta bedriagae
*
63/65
Zootoca vivipara
Podarcis taurica
*
100
*
100
Podarcis muralis
Scelarcis perspicillata
*
89/54
Teira dugesii
68/51
Timon princeps
*
79/
Timon lepidus
*
100
Timon pater
Lacerta agilis
Phoenicolacerta laevis gen. nov.
Iberolacerta bonnali
*
100
Iberolacerta horvathi
Dalmatolacerta oxycephala gen. nov.
*
60/78
Apathya cappadocica
68/-
Hellenolacerta graeca gen. nov.
Anatololacerta danfordi gen. nov.
*
Parvilacerta fraasii gen. nov.
0.05 subs./site
Algyroides marchi
Iranolacerta brandtii gen. nov.
*
Darevskia chlorogaster
*
100
Darevskia saxicola
Lacertini
Lacertinae
Lacertidae

Fig. 20. From Arnold et al. (2007: Fig. 1B): The most actual phylogenetic tree of the Lacertidae comprising in detail the tribe Lacertini (among them *Lacerta* and the new genera *Phoenicolacerta, Dalmatolacerta, Hellenolacerta, Anatololacerta, Iranolacerta*), having been broken up from it). The relationships are indicated by DNA sequences (ML tree from a reanalysis of the mt DNA data set of Harris et al. (1998) based on cytochrome b, 12 S RNA and 16 S RNA). Different probability values resulting from Bayesian analysis are indicated.

The changes in scientific insight are visible by the differences of the earlier drafts and the final hand coloured engraving in Rösel v. Rosenhof's (1758) famous frontispiece (see Fig. 4).

Garsault (1764: pl. 688; fig. 5 hoc loco), a forerunner of Laurenti (1768), and a splitter like him (Chapter 2), moved an almost correct drawing of lacertids forward. In contrast to this figure, Laurenti's (1768: Tab.I, Fig.III) *Seps caerulescens* (= *Lacerta agilis*) has accomplished perfection for the first time in the history of a lacertid drawing. Laurenti's (1768) image remained unique for some decades. Even the excellently hand coloured copper engravings of male and female specimens of *Lacerta agilis* in Wolf in Sturm (1799) and Bechstein (1800) display some deficiencies in pileus scutellation (cf. also Schmidtler 2004). The black / white and coloured engravings in Daudin (1802) are comparably of a very different quality. The colours of his excellently drawn shape of *L. ocellata* (1802: pl. XXXIII; without the blue ocellae) reveals that he did not see a live specimen. But the shape of the adult male is to the point. In Daudin (1801–1803), part of the so called Sonnini edition, for the first time the progressive but extremely expensive technique of colour printing was used in herpetology (see Schmidtler 2007).

On the contrary, the hand coloured engravings in Sonnini & Latreille (1801) are very small – and bad; likewise the figures in the numerous popular editions of the French natural histories, named "Buffon – Cuvier – Lacepède", are out of the question. Their images were cribbed permanently and often lost their quality step-by-step up to an unrecognisable condition.

In the second half of the 19th century research on colours and patterns, the biological reasons and causes of their adaptation, became important for the evaluation of infraspecific variation and biology in general (Eimer, 1881: Taf. XIII–XV). Subsequently, many subspecies, especially within the current genus *Podarcis* (then mostly "*Lacerta lilfordi, Lacerta melisellensis, Lacerta muralis, Lacerta sicula*"), were based upon minute differences in scale counts, colouration and pattern (see Mertens & Wermuth 1960). As a result of the genetic revolution in the last years the importance of naturalistic figures in lacertid systematics is on the decline. At the same time top-quality photos (Fig. 10) have gained in importance especially in popular vivaristic publications.

3.3 Schematic figures

The abstraction of systematically important features, being more or less hidden to the unprejudiced observer, is a condition for successful species recognition. The first noteworthy attempts towards a schematisation of zoological / herpetological features were displayed by Linnaeus in his earlier editions of the "Systema Naturae" (Fig. 11). It is above all the scale counts of ventrals and subcaudals in snakes which are explained in his table III (Linnaeus 1756). Only these scale counts are given in the diagnoses of snakes (see also Linnaeus 1758 and 1766).

The decisive step forward in lizards was made by Merrem (1820). Based upon his similar system in snakes (Merrem 1790, 1820; see Schmidtler 2006) he gave names to the pileus shields of an adult *Lacerta ocellata* (now: *Timon lepidus*; see his page XII and XIII) and depicted their abbreviations in this figure. This description (see Fig. 12) covered seven types of scutes with the letters A (Wirbelschilder – Scuta vertebralia), B (Hinterhauptschilder – Scuta occipitalia), C (Augenbrauenschilder – Scuta superciliaria), E (Stirnschilder – Scuta frontalia posterioria), F (Schnautzenschilder – Scuta frontalia anterioria), G (Rüsselschild – Scutum rostrale, L (Nasenlöcherschilder – Scuta nasalia). This system was later on differentiated and improved by Milne Edwards (1829: pls. 5–8) who depicted and described also the shields of the lower sides of head, body and limbs. The concept of Merrem (1820) and Milne Edwards is valid up to now.

In the middle of the 19th century important osteological investigations also were executed in lacertids. They allowed taxonomic research in the higher categories but also within lacertid genera and species, after a reasonable schematization in osteology, above all in skull terminology, had been found (Fig. 13 from Méhely). They brought about the famous and interminable controversy of L. v. Méhely ("splitter") and G.A. Boulenger ("lumper") on the then intractable "Muralis-Frage" (see Méhely 1909; Boulenger 1920; among others).

It was the research since the middle of the 18th century which revealed the crucial importance of the dorsal pattern especially in the specific and infraspecific taxonomy of the current genus *Podarcis*. Eimer (1881: Taf. XIII; Fig. 14 hoc loco) named the different longitudinal zones ("I bis VI erste bis sechste Zone") which usually exhibit a system of n narrow longitudinal light streaks (nrs. I and III, "Grenzlinien") and dark bands (nrs. II," inneres / äußeres Band"). Méhely (1909: Fig. 1) eased his terminology and gave it the presently valid content. The seven light streaks and dark bands were named after their initial points at the pileus shields (like "Supraciliarstreifen" and "Occipitaband"); see also Schreiber (1912: Fig. 68; p. 333–335) and Mertens (1915: Fig. 3).

Admittedly, morphological schemata (scutellation, dorsal pattern) like these have lost their crucial taxonomic importance in the 19th and 20th centuries during the last two decades because of the reasons given above (see Section 2.2).

3.4 Diagrams

Semi-verbal depictions known in many different shapes (concerning biology as a whole) are book illustrations in broader terms. Contrary to naturalistic figures or the schemata discussed above, phylogenetical trees, based upon genetic research, have become indispensable parts of comprehensive taxonomic work in the last years (Fig. 20). In many analyses the genetic distances currently have totally replaced the traditional taxonomic decisions based upon morphology and reproduction biology – be it appropiate or not.

Tree-like diagrams, comprising also reptiles, trace back to Ray (1693) (see Fig. 15). They have an enormous importance in the history of general biology, not only in lizards. In the field of herpetology, lizards included, they became common practice since the basic works of Duméril (1806) and Oppel (1811; Fig. 16 hoc loco; see also Schmidtler 2009) and Cuvier in Cloquet (1819). Strange to say, it was not clear in those pre-evolutionary times, if the trees should represent identification keys only, or if

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they should depict relationships (too) when illustrating the Linnean hierarchical system by diagrams. Gould (2003: 105) explained the secret of the then triumph of the Linnean categories (from species to class) being nested into one another, by the circumstance that this system later on was capable of being converted into a phylogenetic interpretation (see also Schmidtler 2009: 500, Figs 7a–d).

The subsequent diagrams are not yet phylogenetic trees in a strict sense; especially the one by Kaup (see Fig. 17), who was a follower of the fanciful "natural philosophy". Similar is the quality of Camerano`s diagram (Fig. 18 hoc loco) with its differently sized circles including the phenomenon of resemblances due to morphology.

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A brief history of Greek herpetology

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Abstract. The development of Herpetology in Greece is examined in this paper. After a brief look at the first reports on amphibians and reptiles from antiquity, a short presentation of their deep impact on classical Greek civilization but also on present day traditions is attempted. The main part of the study is dedicated to the presentation of the major herpetologists that studied Greek herpetofauna during the last two centuries through a division into Schools according to researchers' origin. Trends in herpetological research and changes in the anthropogeography of herpetologists are also discussed. Lastly the future tasks of Greek herpetology are presented.

Climate, geological history, geographic position and the long human presence in the area are responsible for shaping the particular features of Greek herpetofauna. Around 15% of the Greek herpetofauna comprises endemic species while 16% represent the only European populations in their range.

THE STUDY OF REPTILES AND AMPHIBIANS IN ANTIQUITY

Greeks from quite early started to describe the natural environment. At the time biological sciences were considered part of philosophical studies hence it was perfectly natural for a philosopher such as Democritus to contemplate "on the Nature of Man" or to write books like the "Causes concerned with Animals" (for a presentation of Democritus' work on nature see Guthrie 1996). The very name of the discipline of herpetology derives from the Greek words *ερπετό* (reptile) and *λόγος* (science) while the term amphibian reflects the typical dual (aquatic and terrestrial) life style of frogs (from the Greek αμφί – both– and *βίος* – life).

The first formal Greek herpetologist was Aristotle himself. In his books on animals (History of Animals, Generation of Animals and On the Parts of Animals) the father of zoology discussed the morphology, physiology and classification of reptiles and amphibians. Nicander was fascinated by the lethal power of snakes, focusing on the venom of serpents in two of his surviving poems (*Theriaca*, *Alexipharmaca*, see Knoefel & Covi 1991).

In late antiquity Pausanias, though he wasn't a naturalist, gave interesting information on the fauna and flora in various locations in Greece through the ten books of his notorious Description of Greece (*Ελλά*δος Περιήγσις). Therein one could find citations to the Greek herpetofauna such as the Seriphian frogs or the tortoises of Arcadia.

REPTILES AND AMPHIBIANS IN GREEK CULTURE

Snake venom and the ability for ecdysis had deeply impressed ancient Greeks who incorporated reptiles in many of their myths. Snakes were considered magical creatures, capable of both good and evil, and were associated with chthonic religious beliefs. In Minoan Crete snakes represented the underworld deities and were worshiped. Tens of statuettes depicting the Goddess of Snakes have been found in excavations all around the island. *Ophion* (from the Greek *ophis* – *όφις* meaning serpent), one of the mighty Titans, was the first ruler of Mount Olympus before he was cast down by Cronus and Rhea. According to legend the first king of Athens, *Kekrops*, was half-snake half-man (διφνής meaning double nature) and thanks to his wisdom he decided to offer his city (known as *Kekropeia* at the time which afterwards changed to Athens to honor the patron goddess) to Athina instead of Poseidon when the two immortals were fighting over its possession. On the other hand Medusa (or *Gorgon*) the mythical monster that had snakes instead of hair, could turn anyone who

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looked at her into stone. *Perseus*, using his shield as mirror, made Medusa look at herself and then decapitated her. He then offered her head to Athina who put it on her own shield (known as *gorgoneion*) so as to petrify her enemies. A serpent-like dragon, *Python*, was sent by Hera after Leto, mother of Apollo and Artemis, to punish her for having an affair with Zeus. Young Apollo took revenge for his mother by killing *Python* at Delphi, where the serpent dwelled. Since then the priestess of the oracle was named *Pythia*. The etymology of the name derives from the verb *pythein* (πύθειν, "to rot"), referred to Python's flesh in the state of decomposition. The priest of Poseidon Laocoon warned the Trojans about the Trojan Horse and tried to convince them to burn it. Athina, who was supporting the Greek army during the War of Troy, sent two snakes to strangle and kill Laocoon together with his sons.

Greeks were aware not only of the lethal power of venom but also of its healing properties. In the statues of *Hygeia*, the goddess of health (the meaning of the word in Greek), a snake is lying on her shoulders. Aesculapius, the god of medicine and son of Apollo, was carrying always his famous rod, a snake-entwined staff (the species was *Zamenis longissimus*). In his most magnificent temple in Epidaurus, that used to function as a hospital, a strange construction known as *tholos* (dome) was erected. Patients spent the night inside *tholos* together with tens of snakes that were believed to heal them. Two small snakes were coiled around Hermes wand, symbolizing the wisdom with which he spoke, since he was considered, together with Athina, god of eloquence.

A fascinating story about the symbolic role of reptiles in antiquity comes from the island of Aegina. During the period of Aegina's naval acme (6th century B.C.) the islanders coined silver staters depicting the sea turtle *Caretta caretta*. However a terrapin (*Testudo* sp.) replaced the sea turtle when the neighboring Athens inaugurated its long period of thalassocracy in Greek seas (after 480 B.C.).

Due to the arid climate Greeks were more familiar with reptiles than amphibians. Thus only few references are known from antiquity, like the Aristophanes' comedy "Frogs" (*βάτραχοι*) or the silver stater that Seriphians coined (ca 530 B.C.) to honor their local hero *Perseus* since frogs were associated with his cult (Pausanias, 2nd century A.D.). Frogs from Serifos Island were famous in antiquity for not croaking (another story linked to Perseus legend) and the expression "Seriphian frogs" was used as a popular proverb during ancient times for people refusing to talk.

With the prevalence of Christianity reptiles become the personification of evil, starting from the Original Sin. Saint George and Saint Demetrius, the so called militant saints, are depicted as dragon slayers, symbolizing the triumph of Good, as expressed by the Greek-Orthodox Church, over Evil, the former idolatry faith. The Serpentine column, dedicated by Greeks in 479 B.C. to Apollo's altar at Delphi to commemorate the victory over the Persians at the battle of Plataea, was formed by three intertwined snakes (Τρικάρηνος *Ό*φις), meaning three-headed snake). Constantine the First moved the column to the Hippodrome of his new capital. However the people of Constantinople destroyed the higher part of the column (the heads of the snakes) since they thought it was the representation of the devil. On the other hand the Apostolic Fathers recognizing the wisdom of snakes were advising the first Christians to be "prudent as the serpent" (Ignatius of Antioch to Polycarp of Smyrna).

Traces of the ancient beliefs still echo in folklore and traditions. The presence of geckoes in a house is considered good fortune. In many households in Cyclades people used to fill with milk a small cup for the "snake of the house" (in Greek σπιτόφιδο, *Zamenis situlus*). The most amazing case though comes from the island of Cephalonia where pagan creeds survive together with christian rituals at the temple of Madonna of the Snakes (Παναγια η φιδουσα). According to the legend a monastery stood at the very same place. When pirates disembarked close to the spot and tried to conquer and harry the treasures of the monastery, nuns prayed for help and Virgin Mary sent snakes that surrounded the building and scared away the pirates. Every year at August the 15th (when Greek Orthodox Church celebrates the Dormition of Holy Mary) locals collect cat snakes (*Telescopus fallax*) days prior to the feast and put them by the icon of the Virgin. Pilgrims touch these snakes and even let them coil around their shoulders or hands since they believe that they will protect them from sickness.

GEOGRAPHY, BIOGEOGRAPHY AND SPECIES RICHNESS

Greece is one of the small European countries with a total area of around 132,000 km^2. However its unique location at the biogeographical crossroads of three continents, each making its distinct biological contribution, makes the country an invaluable site for biodiversity (Lymberakis & Poulakakis 2010). The rough geological mosaic encompassing mountain chains that separate the country into clearly distinct climatic zones and the large number of islands (approximately 8000, most of them in Aegean Sea) have a huge impact on the flora and the fauna (Hausdorf & Hennig 2004). Hundreds of endemic species are hosted in both the mainland and the islands highlighting the region as a hot spot of endemism.

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The climate is typical Mediterranean with long, dry and hot summers and mild winters (though in the north and the mountainous parts of the country winter period could be harsh). These conditions are ideal for reptiles, which thrives in the hospitable Greek habitats but also support various amphibian species and populations. Despite the small size of the country, Greece is home to one of the richest herpetofaunas of Europe hosting 64 species of reptiles and 22 of amphibians. Ten of the reptilian species are endemic and 11 maintain their only European populations in Greece, whereas the respective figures for amphibians are 3 and 2, respectively.

The majority of Greek reptiles and amphibians has Palearctic origin and are common in most of Europe or the Balkans (e.g. *Natrix natrix* or *Bombina bombina*). However, Greece hosts also species of Asian (e.g. *Montivipera xanthina, Lyciasalamandra luschani*) or even African (*Chameleo africanus*) origin. Definitely the most interesting group is the one comprised of the endemic species, the majority of which are islanders, such as *Pelophylax cerigensis*, *Podarcis levendis* or *Macrovipera schweizeri*.

The range and particularities of Greek reptiles and amphibians are, in a considerable degree, the result of the recent geology of the eastern Mediterranean Basin. During the Messinian salinity crisis, the Mediterranean Sea underwent long periods of desiccation that, in Aegean Sea, led to the emergence of landmasses that become islands. The oldest Greek islands (Crete, Skyros and Karpathos) remain to this status even after the Zanclean flood. The Ice Age periods during the Pleistocene with their consecutive freezing and warming conditions had a strong impact on the area, shaping glacial refugia that harbored many cold-intolerant species, which afterwards reinvaded the rest of the Balkans (e.g. *Rana graeca*). Many islands were connected either to mainland Greece or Asia Minor as a consequence of the low sea level during the last Ice Age period. Nowadays the herpetofauna of these islands still reflects this geological incident with islands closer to Greece having a clearly "European" composition (e.g. Evvoia, Thassos), whereas those next to Asia Minor show a more "Asian" character (e.g. Lesvos, Chios, Samos). This separation between European and Asian herpetofaunas is further supported by the existence of a deep-water trench running over the Aegean Sea from southeast to northwest, separating the eastern "Asian" cluster from the western "European" one with only few exemptions. Another important geological factor is the intense volcanism of the region. The Aegean volcanic arch, spanning the southern part of the area, was formed during the Pliocene as a consequence of the northward subduction of the African plate beneath the Aegean one (Fytikas et al. 1984). Milos Archipelago, a small but extremely important in terms of endemism island group, was separated from the rest of the Cyclades by middle Pleistocene as a result of volcanic activity (Sondaar et al. 1986; Dermitzakis 1990).

In summary, most endemic species are concentrated to the oldest islands where the long history of isolation provided the necessary conditions for speciation. The astonishing variety of subspecies in the islands, for instance 19 for *Podarcis erhardii* and 13 for *Cyrtopodion kotshyi* reflects the importance of insularity in the evolution of different morphs. In mainland Greece endemic species are located in the southernmost part of the country, Peloponnese, thanks to historical biogeographical reasons (glacial refugia) matched by a fair period of isolation.

Last, but certainly not least, humans had a significant contribution in shaping the Greek herpetofauna. In the Aegean Sea navigation started quite early (around 9^{th} millenium B.C., Kotsakis 1990; Simmons 1991). Voyagers carried materials (e.g. marble or pottery) that offered an excellent opportunity for transportation of small-bodied species or their hidden eggs (typical examples are *Hemidactylus turcicus* and *Tarentola mauritanica* and most probably *Laudakia stellio*). In some other cases humans may deliberately transport reptiles or amphibians related to religious beliefs. Apart from dispersal, human activities favored reptiles with the deforestation of the largest part of the country, providing opportunities for thermoregulation and foraging. Thousands of kilometers of dry-stone walls all around the country, and especially in the Aegean islands, offer ideal hiding places and support thriving populations. On the other hand touristic development with its accessory consequences (water over-pumping, wetland drainage, habitat degradation), over grazing and intensive agriculture has largely altered the landscape, influencing negatively upon reptiles and, mostly, amphibians.

THE FRENCH MOREA EXPEDITION

The Morea (the Greek vernacular name for Peloponnese) Expedition (French: *Expédition de Morée*) accomplished by the French Army at the end of the Greek War of Independence. After the naval battle of Navarino where the united Franco-Russo-British fleet destroyed the Ottoman fleet, French expeditionary corps disembarked at southern Peloponnese to secure the evacuation of the area from the Turks. Following the example of the successful Napoleon's Egyptian Campaign where a scientific committee accompanied the French troops, a scientific mission escorted the expedition in Peloponnese. The Head of the 17 experts of different disciplines that comprised the mission was the naturalist Jean Baptiste Bory de Saint Vincent. Bory collected hundreds of plants and animals that were sent to France for further identification and classi-

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fication. It was from these specimens that the herpetology of Greece began formally in 1833, when the first endemic species to Peloponnese were described by Bory and his colleague Gabriel Bibron, who also participated in the Morea expedition. Bibron worked extensively on Herpetology and helped his mentor Duméril in the publication of the first herpetological monograph *Erpétologie générale* (1834-–1854) where many species distributed in Greece were described.

The Morea Expedition covered not only Peloponnese but also numerous Greek islands. The importance of this mission was crucial and later studies on Greek herpetofauna were largely based on the Expedition's observation. Bibron and Bory described in total three species (*Algyroides moreoticus, Podarcis peloponnesiacus* and *Ophiomorus punctatissimus*), while later Duméril and Bibron, using specimens from Corfu, described one species (*Algyroides nigropunctatus*).

THE GERMAN SCHOOL

It is widely accepted that Greek herpetology, at least during its early period, literally "spoke German". Eminent herpetologists from Germany, Austria and Switzerland worked (and are still working) extensively on Greek reptiles and amphibians, setting the basis for herpetology in the country. Maybe the underlying reason should be seeked in the first king after the War of Independence, Otto the First, son of Ludwig of Bavaria (Wittelsbach House), who brought with him hundreds of Germans to staff the administration of the new country. In this session the most important contributions in Greek herpetology were presented.

The first German naturalists who arrived in the country and presented information on Greek amphibians and reptiles were not herpetologists but ornithologists (Erhard, Reiser) or botanists (Heldreich, Herzog). Hence many of their first observations proved to be incorrect since they were not familiar with herpetological systematics.

Jacques von Bedriaga wrote the first major monograph on Greek reptiles and amphibians in 1881. After receiving his PhD Thesis from the University of Jena he started to travel very frequently to both Italy and Greece. The fruits of these trips was his "Die Amphibien und Reptilien Griechenlands" which was published in Moscow in three volumes. His special interest on lacertids is best reflected in the description of four new species, two of which are endemic to Peloponnese and Milos Island (namely *Hellenolacerta graeca*, *Podarcis milensis*, *Lacerta trilineata* and *P. erhardii*). Though Bedriaga was born in Russia, where he also took his bachelor's degree at the University of Moscow, he became scientifically active in Germany and published most of his works in German. That's why his name is herein included in the so-called German School.

Oskar Boettger, though never visited Greece, made the second important contribution to Greek herpetology. During the years he was infirm and remained at home, he received numerous specimens sent by his many friends and colleagues. Among them von Oertzen shipped him reptiles and amphibians he collected while in Greece. Boettger worked on this collection and later published his findings (1888, 1891).

On of the most prominent European herpetologists, Robert Mertens, worked also on the Greek herpetofauna. He realized at least three herpetological excursions in the country, which later resulted in a series of paper (1959, 1961, 1968a, 1972). Using types and specimens from the large collections of the Senckenberg Museum in Frankfurt he also wrote systematics articles (1955, 1968b). His most significant contribution though, was the publication, together with Müller (1928, 1940) and Wermuth (1960), of the European checklists of amphibians and reptiles. This book has been a useful reference for researchers of the Greek herpetofauna. At this point it is worthy of mentioning that Müller himself contributed one of the first herpetological papers on Greek herpetofauna in 1908.

Karl Buchholz and Ulrich Gruber, both curators of herpetology in the Zoologisches Forschungsmuseum Alexander Koenig (hereinafter ZFMK), dedicated a large part of their research on Greek reptiles and especially to the island populations. Buchholz undertook numerous herpetological excursions to Greece and collected many specimens (being an excellent markeman he shot his targets from long distance). His collections were published in a series of paper on the Aegean reptiles (1960, 1961, 1962a,b). Gruber focused also on insular populations (Gruber & Fuchs 1977, Gruber 1979) and following Werner's example, specialized in the North Sporades island group (Gruber & Schultze-Westrum 1971, Gruber 1986).

Hans Schneider, one of the leading researchers of amphibians, worked closely with Sofianidou and Kyriakopoulou-Sklavounou analyzing the acoustic properties of various species of frogs (1984, 1985, 1988, 1993). Acknowledging the impact of his research on Greek herpetology he was invited as the pleninary speaker at the 10th Meeting of *Societas Europea Herpetologica* in Crete in 1999 (Bioacoustic studies in European Anurans).

Many more German herpetologists, professional or amateurs, did research on Greek species and it would be impossible to mention all of them in this brief paper. In any case it would be an omission not to mentioned B. Schneider who reported on the herpetofaunas of many Greek islands (e.g. 1986, 1995), A. Beutler who was interested also in insular populations (1979, Beutler & Froer 1980) and B. Trapp who investigated the Greek population of *Chamaeleo africanus* (e.g. 2003, 2004) and also wrote a book on Greek amphibians and reptiles in German (2006).

Wolfgang Böhme is maybe the last of the Mohicans of the one-time all-potent German School. His engagement with Greek herpetofauna dates back to the time he was a student at the Christian-Albrechts University of Kiel. At 1969 he traveled with a friend to the Syrian borders of Turkey. On their way back they visited Thessaloniki and planned a field trip to study the endemic species of Peloponnese. Unfortunately their old Volkswagen "beetle" let them down in Athens so they had to cancel their excursion until the engine could be fixed. However they didn't waste their time and attempted a herpetological survey of the area surrounding Acropolis. Their persistence was rewarded with observations on *Chalcides occelatus* and *Zamenis situlus* while they also discovered a dense population of *Lacerta trilineata* (specimens of this population can be found in the collections of ZFMK).

In 1971 Wolfgang Böhme took office as Curator of the Herpetological Collection in ZFMK. His predecessors, Karl Buchholz and Ulrich Gruber, were keenly interested in Greek herpetofauna, as mentioned above, and thus enhanced considerably the collections of the Museum. Thanks to them the newly appointed Böhme was able to immerse himself in the Greek collections during his curatorship. It was in a series of *Pseudepidalea viridis* specimens collected by Buchholz in Peloponnese that Böhme discovered two misplaced adult individuals of *Pelobates syriacus*, the first record of this species in Greece (1975).

The aborted field trip to Peloponnese finally took place in 1996, after his participation in the Congress of the Hellenic Zoological Society in Athens where he presented a paper on the Cypriot herpetofauna. During this trip Böhme went to Sparta and Mystras and observed many endemic species *in situ*. But another chance to visit Peloponnese would come from the far past.

The former director of ZFMK, the archeozoologist Günther Nobis, had a house near Pylos. During his vacations he shot a black-and-white photo of a chameleon and upon his return to Bonn gave it to Böhme. Since morphological details were not discernible, Böhme assumed it to be *C. chamaeleon* and consequently published this record in a brief note (1989). In 1997 Böhme visited Nobis so as to have a first-hand examination of the species. During this visit he met Andrea Bonetti and George Chiras who led him to the chameleon habitat where they soon detected the first male individual. To their surprise instead of the typical small occipital flaps of *C. chamaeleon*, they found a tarsal spur, characteristic of the African species *C. africanus*. At the time the range of this species was believed to be restricted only to Africa. Böhme and his colleagues assumed that *C. africanus* was introduced to the area as result of the trade between Alexandria and Pylos, since the Gialova lagoon (the only place where the African chameleon is distributed in the country) is located to the exact site of the former ancient harbor of Nestor's Palace (Böhme et al. 1998). The results were later verified with mtDNA analysis (Kosuch et al. 1999). This fascinating discovery came to corroborate the human influence on species dispersal in the Mediterranean Sea.

Together with Evgeny Roitberg and his former PhD student Andreas Schmitz, now curator of herpetology in Geneva, Böhme traveled to Greece once more in 1999 to attend the 10th Meeting of SEH in Iraklion, Crete. They made herpetological observations in Macedonia and at Mount Olympos. The last SEH Meeting in Kussadasi (2009) gave another opportunity to visit Greece. On his way back from Turkey, Böhme stopped, with his phd student Philipp Wagner, at various localities in northeastern Greece (Thrace and Macedonia).

Last, but certainly not least, the impact of the *Handbuch der Amphibien und Reptilien Europas* (1981, 1984, 1986, 1993a) in which Böhme edited the volumes for snakes and lizards (and also contributed personally some species accounts – 1984, 1993b,c), has been catalytic for the development of herpetology in Greece. Data on ecology, systematics, physiology and behavior were for the first time gathered and accessible to researchers.

Besides the above, Wolfgang Böhme has another, more "indirect", nonetheless important, relationship with Greek herpetology. During all the years he served as Head of the Herpetology Section in ZFMK (1971–2010) and Vice Director of the Museum, he facilitated in every possible way researchers who were working on specimens from Greece. Many Greek herpetologists visited numerous times the rich herpetological collections of the Museum and retrieved valuable information on diet, reproduction, morphology, ontogeny, intra- and inter-population variation, anatomy and phylogeny of Greek amphibians and reptiles. These data led to the publication of various scientific papers that considerably enlarged our knowledge of the Greek herpetofauna.

THE AUSTRIAN SCHOOL

Franz Werner was one of the most prolific and influential herpetologists who worked on Greek amphibians and reptiles. Starting from 1894 he was an avid and consistent researcher of Greek herpetofauna and remained active till his death (1939), publishing a series of papers (1912, 1927, 1933, 1937, 1938). He was the first to describe the herpetofauna of Ioanian islands (1894) and he also expanded his studies to the Aegean Sea. Maybe his most important manuscript was the one published in English, something quite unusual for a German-speaking scientist at the time, by the University of Michigan (1930). Therein he describes the findings of the visit he made at some Aegean Islands in 1927. In this mission he had the chance to collaborate with K.H. Rechinger while informative photos shot by Prof. Schoenwetter illustrated the final paper. In his long herpetological pursuits in Greece Werner described four new species: *Lacerta anatolica*, *L. oertzeni* (a tribute to von Oertzen), *Podarcis gaigeae* (endemic to Skyros Archipelago and dedicated to Helen Gaige) and *Macrovipera schweizeri*. After his death his sons donated his huge personal collection to the Natural History Museum of Vienna, which since then is one of the wealthier in specimens coming from Greece.

Werner's pupil Otto von Wettstein followed up with enthusiasm the work of his teacher on Greek reptiles. He took over as Curator of vertebrates at the Natural History Museum of Vienna in 1920 and published his first paper on the herpetofauna of Crete in 1931. In his studies he emphasized the reptilian and amphibian populations of the Aegean islands of which he was a regular visitor. In 1942 he participated in a scientific mission to Crete that was conducted by a German Wehrmacht biological research squad. Without doubt his most important paper was the emblematic *Herpetologia Aegea* (1953). In the 182 pages of this landmark effort, Wettstein presented in the most detailed way, full of knowledge, all the information on the zoogeography of the Aegean Sea herpetofauna.

The legacy Wettstein left to the Natural History Museum of Vienna is enormous and, luckily, his interest in Greek herpetofauna survived among his successors till today. Heinz Grillitsch, the actual Head of the Herpetological Collection since 1984, investigated aspects of the Greek herpetofauna (Grillitsch & Tiedemann 1984, Grillitsch & Cabela 1990, Grillitsch & Grillitsch 1991). Within his responsibilities lies the heavy burden to maintain and preserve the huge collection, one of the greatest in Greek specimens. Werner Mayer from the molecular systematic lab of the Museum has been working on the ecology and distribution of reptiles and continues to study the phylogenetic relationships of numerous Greek lizards (Mayer 1986, 1993, Mayer & Beyerlein 2002, Mayer & Arribas 2003). Franz Tiedemann, who is collaborating closely with the Museum, has conducted numerous studies on various aspects of herpetology on Greek species (e.g. Tiedemann & Häupl 1980, 1982, Tiedemann & Grillitsch 1986).

There are many more Austrian herpetologists that need to be mentioned here like Peter Keymar, who frequently visited Greece and published papers on Greek amphibians and reptiles (1984, 1986a, b, 1988) or Thomas Bader and Christoph Riegler (2004, 2009) who described the herpetofauna composition of Rhodes Island. A special citation should be made to the very active Austrian herpetological group *www.herpetofauna.at*. In their excellent website one may find a wide variety of photos of Greek reptiles and amphibians since the members of the group have repeatedly visited Greece.

THE "INTERNATIONAL BRIGADES"

Besides the predominant German and Austrian Schools that shaped the history of Greek herpetology, researchers from many other European countries made important contributions to the study of amphibians and reptiles of the country.

Dodecanese islands during the first decades of the 20th century were under Italian rule and Italian naturalists described the herpetofauna of the region. Enrico Festa of the Museum of Zoology in Turin made herpetological observations in the island of Rhodes that later were published by Calabresi (1923b) who also write his impression of a survey on Samos Islands (1923b). At the same period Ettore Zavattari published a study on the fauna of the "Italian islands of the Aegean Sea" (1929). Augusto Cattaneo is one of the most prolific authors on the distribution of Greek reptiles and amphibians, especially in the insular country (e.g. 1984, 1997, 1999, 2007). Another Italian herpetologist who investigated the range of Greek herpetofauna is Pierangelo Crucitti (e.g. 1990).

The United Kingdom is represented by a handful of very productive herpetologists. Adrian Hailey (now at the University of West Indies, Trinidad and Tobago), who worked for a long period at the University of Thessaloniki, emphasized his research on the tortoise populations in Greece (e.g. Hailey 2000, Hailey & Willemsen 2003) while he also examined the metabolism of *Laudakia stellio* in collaboration with Nikos Loumbourdis. Richard Clark wins easily the title of the champion of publications on the distribution of Greek amphibians and reptiles. Starting from 1967 he wrote over 20 papers (e.g. 1968, 1971, 1989, 1996, 2000) covering most places of the country. Finally David Buttle traveled around Greece and published many new localities regarding the distribution of Greek herpetofauna (e.g. 1989, 1994, 1997). Nicholas Arnold with the different editions of his excellent guide on European amphibians and reptiles (1985, 2004) offered an important reference book to herpetologists working on Greek species.

In the 1970's Hans Lotze did many field trips in Greece and gave considerable information about snakes (e.g. 1974, 1977). Peter Beerli of Florida State University studied Aegean water frogs (Beerli et al. 1996) and even described two new endemic species using molecular biology tools (Beerli et al. 1994): *Pelophylax cerigensis* and *Pelophylax cretensis*. But the real star of Swiss herpetologists that involved the study of Greek species was undoubtedly Hans Schweizer, the famous "Schlangenhansi". Schweizer, an amateur herpetologist with a particular preference to vipers, had already a reputation among the European herpetological community when in 1931 visited Milos Island. After spending considerable time walking throughout the island and observing lizards and snakes, he noted the striking differences between the local and mainland herpetofaunas. He begun to publish his findings (1932, 1935, 1938, 1957) and also contacted professional herpetologists around Europe, with whom he had a regular correspondance, and started sending specimens. It was from one of those samples that Müller described the endemic Milos grass snake in 1932 and dedicated it to him (*Natrix natrix schweizeri*). Thanks to Schweizer, Milos Island gained its reknown as herpetological hot spot in Mediterranean. Besides the grass snake, two more species bear Schlangenhansi's name: *Macrovipera schweizeri* and *Lacerta trilineata hansschweizeri*.

Otto Cyrén, one of the pioneers of Greek herpetology, was born in Sweden but spent many years of his life in Germany and consequently wrote in German his papers on Greek and Balkan herpetofauna (1928, 1933, 1935). Göran Nilson of Göteborg University, a viper expert, has examined various aspects of the biology of *Macrovipera schweizeri* with his Greek collaborators Dimaki, Ioannidis and Dimitropoulos (Andren et al. 1994, Nilson et al. 1999). A younger representative of Swedish herpetology is Anna Runemark of Lund University who is doing her PhD thesis on the sexual isolation between mainland and inland populations of *Podarcis gaigeae* (Runemark et al. 2008).

Two herpetologists from the Netherlands have studied the Greek herpetofauna. Ronald Willemsen focused on the study of Mediterranean tortoises (e.g. Willemsen 1991, 1999, Willemsen & Hailey 2002) while Henk Strijbosch examined the distribution and ecology of lacertids (Strijbosch et al. 1989, Strijbosch 2001).

The Czechoslovakian Stepanek traveled to Greece and published an important contribution to the knowledge of Greek herpetofauna in 1944, along with two other papers (1934, 1938). Mario Broggi from Liechtenstein is a regular visitor to Greece and has published over 15 papers on local herpetofaunas around the country (e.g. 1978, 1988, 1997, 2009). The Danish Henrik Bringsøe is another researcher that wrote on different species of reptiles and amphibians (e.g. 1986, 1997, 2004). Jeroen Speybroeck from Belgium has visited Greece many times and runs a well organized website with great photographs of Greek amphibians and reptiles (http://www.hylawerkgroep.be/jeroen).

GREEKS ON GREEK HERPETOLOGY

Until the late 1960's only foreign scientists, mostly from Central Europe, were researching on the Greek herpetofauna. In 1968 John Ondrias of the University of Patras (which hosts the oldest School of Biology in Greece) published the first list of amphibians and reptiles. That was the starting point that instigated many Greek zoologists to get involved in herpetological studies. Theodora Sofianidou of the University of Thessaloniki carried out the first dissertation on herpetology in 1977. Since then 18 researchers defended their PhD theses on herpetological subjects. Namely (in order of seniority): Loumbourdis (1981), Kyriakopoulou-Sklavounou (1983), Xyda (1983), Chondropoulos (1984), Tzannetatou-Polymeni (1988), Valakos (1990), Asimakopoulos (1992), Maragou (1997), Adamopoulou (1999), Vassara (1999), Kassapidis (2001), Poulakakis (2003), Pafilis (2003), Tsiora (2003), Sotiropoulos (2004), Mantziou (2006), Dimaki (2007) and Simou (2009).

Bassilis Chondropoulos published the checklists of Greek lizards and snakes in 1986 and 1989 respectively. These papers remained for a long period the most dependable source for the distribution of the Greek herpetofauna. Sofianidou wrote the first complete herpetological monograph in Greek in 1999 on *Testudo marginata*. In 2000 Achilleas Dimitropoulos and Yannis Ioannides published their work on the reptiles of Greece and Cyprus (in Greek), the first herpetological book to appear in Greece.

Nowadays Greek herpetologists are working under the auspices of Universities, non-governmental organizations and Museums. The major groups of herpetological research are located at three Universities. At the University of Athens (the oldest in the country) Professors of Ecology Ioannis Matsakis and Moisis Mylonas though not herpetologists encourage young people to work in the field and do indepth research during preparations of their dissertation. Rosa Maria Tzannetatou-Polymeni and Sratis Valakos, pupils of the aforementioned, became faculty in 1990 and 1992 respectively and with their turn supervised new herpetological PhD theses. Tzannetatou-Polymeni (assistant professor) is an expert on both *Lyciasalamandra* species and is actually supervising a PhD thesis on the endemic Helversen's salamander (Karpathos and Kassos islands). Valakos (associate professor) laid a foundation for an active group that has already produced five dissertations while two more are in process. Together with colleagues from other institutions he published an accomplished guide for the amphibians and reptiles of Greece (in English) in 2008. Earlier, with his collaborators, wrote the first volume on a local herpetofauna (2004, in both Greek and English). His research focuses on the environmental physiology and phylogeny of lacertid lizards (e.g. Valakos 1989, Valakos & Mylonas 1992, Valakos et al. 2007). Angeliki Xyda, former faculty (now retired), conducted studies on the ecology of *Laudakia stellio* (e.g. 1986).

Professor Mylonas moved to the University of Crete at 1992 and set the basis for a new herpetological nucleus. Three dissertations have been completed so far whereas more PhD candidates are still working on their theses. Petros Lymberakis, curator of vertebrates at the Natural History Museum of Crete (belonging to the University of Crete) deals with numerous aspects of herpetology (e.g. Lymberakis et al. 2007, 2008). Nikos Poulakakis (assistant professor) has worked extensively on the reconstruction of the phylogenetic histories of various amphibians and reptiles (e.g. Poulakakis et al. 2003, 2005a, b, 2008).

At the Aristotelian University of Thessaloniki the research group of Sofianidou and Kyriakopoulou-Sklavounou began a series of papers on frogs in collaboration with Hans Schneider. Fruit of their work, based on bioacoustics, was the description of a new species (*Pelophylax epeiroticus* – 1984). Sofianidou (now retired) supervised two dissertations and worked mainly with amphibians (e.g. Sofianidou & Kyriakopoulou-Sklavounou 1983, Sofianidou 1996). She was also one of the editors and main contributors to the Atlas of Amphibians and Reptiles in Europe (Gasc et al. 1997). Kyriakopoulou-Sklavounou (associate professor) supervised one PhD thesis while studying life-history traits and genetic differentiation of Greek frogs (e.g. Kyriakopoulou-Sklavounou 1992, Kyriakopoulou-Sklavounou et al. 2000, 2003). Nikos Loumbourdis (professor) studies the metabolism and overall physiology of amphibians and reptiles (e.g. Loumbourdis & Hailey 1985, Loumbourdis 1997, 2005, 2007).

Besides the aforementioned foundations the Goulandris Natural History Museum hosts a group of active herpetologists: Dimitropoulos who contributed many new localities for reptiles (e.g. 1986, 1990), Ioannides wrote on the herpetofaunas of numerous areas and also on the ecology of reptiles (e.g. Ioannides et al. 1994, Ioannides & Bousbouras 1997) and Maria Dimaki, who has focused on chameleons (e.g. Dimaki et al. 2000a,b). Panayiota Maragou of the WWF Hellas studies the ecology of lacertids endemic to Peloponnese (e.g. Maragou et al. 1996, 1999), while Chloe Adamopoulou (Zoological Museum of the University of Athens) is emphasizing on *Podarcis milensis* (e.g. Adamopoulou et al. 1999, Adamopoulou & Valakos 2005). Dimitris Margaritoulis of *Archelon* did an important work on the conservation of sea turtles (e.g. Margaritoulis et al. 1986, Margaritoulis 2005).

US based Greek Johannes Foufopoulos (assistant professor, University of Michigan) is investigating the evolution and physiological adaptations of lizards on islands of Aegean Sea (e.g. Foufopoulos 1997, Foufopoulos & Ives 1999) in close collaboration with herpetologists in Greece. Recently two more members of the Greek herpetological community became faculty: Konstantinos Sotiropoulos (University of Ioannina, lecturer) who studies genetic differentiation and phylogenetic relations in newts (e.g. Sotiropoulos et al. 2001, 2008a,b, 2009) and Panayiotis Pafilis (University of Athens, assistant professor), focusing on functional ecology and conservation physiology of lacertids (e.g. Pafilis et al. 2005, 2007, 2008, 2009).

The increasing number of people involved in herpetological studies in Greece is also reflected in the organization of three Congresses: the First (1992) and the Sixth (2008) Symposia on the Lacertids of the Mediterranean Basin (both held in Lesvos Island) and the 10th Ordinary General Meeting of SEH in Crete (1999). Some of the contributions presented during the last were published in a volume under the general title *Hereptologia Candiana* (Lymberakis et al. 2001).

The threatened species of the Greek herpetofauna have been recorded in the two editions of the Red Data Book of threatened species of Greece. In the first edition (Karandinos & Paraschi 1992) eight species (seven reptiles and one salamander) are listed as threatened while in the second edition (Legakis & Maragou 2009) twelve reptiles and six amphibians are characterized as critically endangered, endangered or vulnerable.

An important step in the history of Greek Herpetology was the foundation of the Hellenic Herpetological Society (*Societas Herpetologica Hellenica*, Ελληνική Ερπετολογική *Εταιρεία* – http://www.elerpe.org) in 2000. The members of the Society are scientists who are involved in the study of amphibians and reptiles but also amateur herpetologists (as non-full members) who are interested in conservation and natural history. At this point *Archelon*, the Sea Turtle Protection Society of Greece (http://www.archelon.gr), should be mentioned as well. Thanks to the efforts of this pioneer group (founded on early 1980's), Greek public opinion was sensitized towards the conservation of *Caretta caretta*.

PAST, PRESENT AND FUTURE OF GREEK HERPETOLOGY

Unlike herpetologies of other European countries, herpetological publications in Greece up to the 1970's dealt with systematics, focusing on the discovery and description of new species. The majority of studies concerned the distribution of various taxa and the description of local herpetofaunas, with emphasis on the islands. Nonetheless, during the last decade, herpetologists are covering successfully a wide spectrum of biological aspects including molecular biology, genetic differentiation, environmental physiology, functional ecology, immunology and the overall picture has been reversed (Fig. 1).

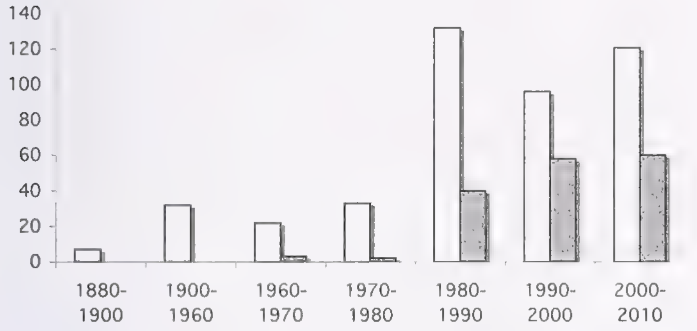

Fig. 1. Histogram of publications (total 606 papers) made by foreign (light bar) and Greek herpetologists (spotted bar).

The number of species inhabiting Greece has been raised throughout the years (see Appendix I). During the first two decades of 19th century only the species described by the classical taxonomists (Linnaeus, Laurenti and Pallas) were known from Greece. The French Morea Expendition led to the description of the first endemic species and since then the study of the Greek herpetofauna became methodical and continuous. New species are rather rare and their description is based on cutting edge technology tools, like molecular inference, paired though with typical anatomical-morphological studies (e.g. Beerli et al. 1994). This is also the case for the recently described lacertids *Podarcis cretensis* and *P. levendis*, the first Greek species that were published by an exclusively Greek group (Lymberakis et al. 2008).

Until today foreign researchers were publishing most of the papers on the Greek herpetofauna. However this trend has changed during the last 20 years and today the scientific work of Greek herpetologists has yielded a continuously growing number of papers (Fig. 2). It is important to mention that most Greek researchers are working in collaboration with colleagues from Europe and North America, keeping alive the international interest for the Greek herpetofauna and exchanging ideas and methods.

Habitat degradation, environmental pollution, introduced species and the non-stop, greedy development of tourism (principal source of money for Greek economy) stress the imperious need for conservation studies in the immediate future. Though knowledge of species distribution is in satisfactory level, the evaluation of populations' status is still very poor. Amphibian and fresh water turtle populations are known to decrease as a consequence of water pollution and the desiccation of water bodies. The problem is much more intense in the islands because of tourism-related activities (excessive withdrawal of groundwater and construction projects on wetlands areas). Reptile populations are threatened by wildfires that the last 10 years destroyed a significant part of Greek forests and also, in the case of small islets, by overgrazing. Greece hosts some very important nesting beaches for *Caretta caretta*, endangered as well by tourism and fishing. In order to protect and maintain one of the richest European herpetofaunas special conservation projects should be undertaken shortly with the contribution of herpetologists from all fields.

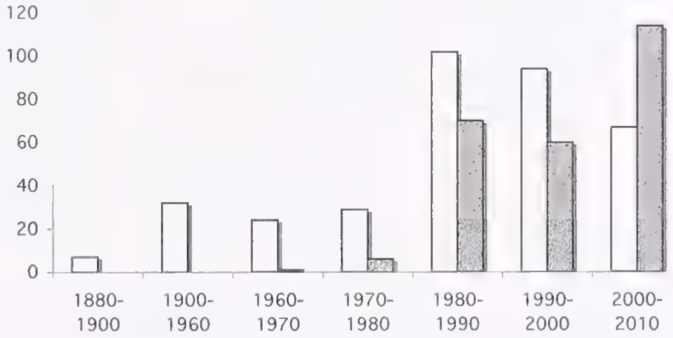

Fig. 2. Chart of publications concerning systematics and distribution (light bar) and non-systematic and distributional records (spotted bar) of a total of 606 papers.

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APPENDIX

Table 1. List of species known from Greece with distribution and date of original description.

Date	Species	Author	Range	Group
1758	*Anguis fragilis*	Linnaeus	Mainland Greece, Thassos and Corfu islands	Rept: Anguidae
1758	*Bombina variegata*	Linnaeus	Mainland Greece, not in Peloponnese	Amph: Discoglossidae
1758	*Bufo bufo*	Linnaeus	Mainland Greece and large Aegean islands	Amph: Bufonidae
1758	*Caretta caretta*	Linnaeus	All Greek seas	Rept: Cheloniidae
1758	*Chamaeleo chamaeleon*	Linnaeus	Chios and Samos Islands	Rept: Chamaeleonidae
1758	*Chelonia mydas*	Linnaeus	All Greek seas	Rept: Cheloniidae
1758	*Dolichophis jugularis*	Linnaeus	Islands of southeastern Aegean Sea	Rept: Colubridae
1758	*Emys orbicularis*	Linnaeus	Mainland Greece, Samos, Samothraki, Kos, Lesvos and Evvoia islands	Rept: Emydidae
1758	*Eryx jaculus*	Linnaeus	Throughout the country excluding Crete	Rept: Boidae
1758	*Hemidactylus turcicus*	Linnaeus	Throughout the country	Rept: Gekkonidae
1758	*Hyla arborea*	Linnaeus	Mainland Greece and large islands	Amph: Hylidae
1758	*Lacerta agilis*	Linnaeus	Northern borders in high elevations	Rept: Lacertidae
1758	*Laudakia stellio*	Linnaeus	Only European population Eastern Aegean Sea Islands, Corfu, Thessaloniki and central Cyclades	Rept: Agamidae
1758	*Lissotriton vulgaris*	Linnaeus	Mainland Greece and large Ionian islands	Amph: Salamandridae
1758	*Natrix natrix*	Linnaeus	Throughout the country excluding Crete	Rept: Colubridae
1758	*Rana temporaria*	Linnaeus	Northern borders with Bulgaria	Amph: Ranidae
1758	*Salamandra salamandra*	Linnaeus	Mainland Greece	Amph: Salamandridae
1758	*Tarentola mauritanica*	Linnaeus	Western Peloponnese, Crete and Ionian Islands	Rept: Gekkonidae
1758	*Testudo graeca*	Linnaeus	Mainland Greece and many islands	Rept: Testudinidae
1758	*Trionyx triunguis*	Forsskål	Introduced, Kos island	Rept: Trionychidae
1758	*Trachylepis auratus*	Linnaeus	Rhodes, Kos, Symi and Samos islands	Rept: Scincidae
1758	*Vipera ammodytes*	Linnaeus	Throughout the country excluding Crete, Milos Archipelago and eastern Aegean Sea islands	Rept: Viperidae
1758	*Vipera berus*	Linnaeus	Macedonia and Thrace in high elevations	Rept: Viperidae
1758	*Zamenis situlus*	Linnaeus	Throughout the country	Rept: Colubridae
1761	*Bombina bombina*	Linnaeus	Borders with Bulgaria, River Evros	Amph: Discoglossidae
1761	*Dermochelys coriacea*	Vandelli	All Greek seas	Rept: Dermochelyidae
1768	*Chamaeleo africanus*	Laurenti	Only European population, a restricted zone in southeastern Peloponnese	Rept: Chamaeleonidae
1768	*Coronella austriaca*	Laurenti	Epirus, Macedonia, Thrace, Thassos and Samothraki islands	Rept: Colubridae
1768	*Hierophis gemonensis*	Laurenti	Throughout mainland Greece excluding Macedonia and Epirus, Ionian islands and Crete	Rept: Colubridae

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Date	Species	Author	Range	Group
1768	*Lacerta viridis*	Laurenti	Mainland Greece excluding Peloponnese	Rept: Lacertidae
1768	*Mesotriton alpestris*	Laurenti	Mainland Greece	Amph: Salamandridae
1768	*Natrix tessellata*	Laurenti	Throughout the mainland country, Crete and some Aegean and Ionian islands	Rept: Colubridae
1768	*Podarcis muralis*	Laurenti	Throughout mainland Greece and Thassos island	Rept: Lacertidae
1768	*Pseudepidalea viridis*	Laurenti	Mainland and insular Greece	Amph: Bufonidae
1768	*Triturus carnifex*	Laurenti	Epirus, Macedonia and Corfu island	Amph: Salamandridae
1768	*Zamenis longissimus*	Laurenti	Throughout the mainland country, Corfu and Paxoi islands	Rept: Colubridae
1774	*Pelophylax ridibundus*	Pallas	Eastern Macedonia and Thrace	Amph: Ranidae
1775	*Chalcides ocellatus*	Forsskål	Attica and close islands, Crete, eastern Peloponnese	Rept: Scincidae
1775	*Pseudopus apodus*	Pallas	Mainland Greece and in many large islands	Rept: Anguidae
1789	*Dolichophis caspius*	Gmelin	Throughout the country excluding Crete, Rhodes and the majority of Peloponnese	Rept: Colubridae
1789	*Elaphe quatorlineata*	Lacepède	Throughout the country excluding Crete and Rhodes	Rept: Colubridae
1789	*Eurotestudo hermanni*	Gmelin	Mainland Greece, Zakynthos, Cephalonia, Corfu and Evvoia islands	Rept: Testudinidae
1789	*Hierophis viridiflavus*	Lacepède	Introduced, Gyaros Island	Rept: Colubridae
1789	*Platyceps najadum*	Gmelin	Throughout the mainland country and in some Aegean islands	Rept: Colubridae
1795	*Testudo marginata*	Schoepff	**Endemic**, Mainland Greece excluding Thrace and many Aegean islands	Rept: Testudinidae
1802	*Rana catesbeiana*	Shaw	Introduced, Crete	Amph: Ranidae
1804	*Malpolon monspessulanus*	Hermann	Throughout the country excluding Crete and Cyclades	Rept: Colubridae
1814	*Elaphe sauromates*	Pallas	Thrace and Thassos island	Rept: Colubridae
1814	*Podarcis tauricus*	Pallas	Throughout mainland Greece and Ionian islands	Rept: Lacertidae
1820	*Typhlops vermicularis*	Merrem	Throughout the country excluding Crete	Rept: Typhlopidae
1831	*Telescopus fallax*	Fleischmann	Throughout the country	Rept: Colubridae
1832	*Ophisops elegans*	Ménétriés	Only European population, islands of northeastern Aegean Sea	Rept: Lacertidae
1833	*Ablepharus kitaibelii*	Bibron & Bory	Throughout the country / terra typica in Greece	Rept: Scincidae
1833	*Algyroides moreoticus*	Bibron & Bory	**Endemic**, Peloponnese and few Ionian Islands	Rept: Lacertidae
1833	*Mauremys rivulata*	Valenciennes	Throughout the country	Rept: Geoemydidae
1833	*Ophiomorus punctatissimus*	Bibron & Bory	Only European population, Peloponnese, Kythira and Kastelorizo islands / terra typica in Greece	Rept: Scincidae
1834	*Darevskia praticola*	Evermann	Eastern Thrace near river Evros	Rept: Lacertidae
1834	*Hemorrhois nummifer*	Reuss	Only European population, Islands of southeastern Aegean Sea	Rept: Colubridae
1833	*Podarcis peloponnesiacus*	Bibron & Bory	**Endemic**, Peloponnese / terra typica in Greece	Rept: Lacertidae
1835	*Vipera ursinii*	Bonaparte	Central and northern Greece in high elevations	Rept: Viperidae
1838	*Eirenis modestus*	Martin	Only European population, Thrace and eastern Aegean Sea islands	Rept: Colubridae
1839	*Algyroides nigropunctatus*	Duméril & Bibron	Western mainland Greece (excluding Peloponnese) and Ioanian Islands / terra typica in Greece	Rept: Lacertidae
1840	*Rana dalmatina*	Bonaparte	Discontinuous range in mainland Greece	Amph: Ranidae

Date	Species	Author	Range	Group
1849	*Montivipera xanthina*	Gray	Only European population, Thrace and eastern Aegean Sea islands	Rept: Viperidae
1870	*Cyrtopodion kotschyi*	Steindachner	Throughout the country	Rept: Gekkonidae
1870	*Trituris karelinii*	Strauch	Macedonia and Thrace	Amph: Salamandridae
1876	*Podarcis erhardii*	Bedriaga	Throughout mainland Greece, Sporades and Cyclades / terra typica in Greece	Rept: Lacertidae
1881	*Hellenolacerta graeca*	Bedriaga	**Endemic**, Peloponnese	Rept: Lacertidae
1882	*Pelophylax bedriagae*	Camerano	River Evros, east Aegean Islands	Amph: Ranidae
1882	*Podarcis milensis*	Bedriaga	**Endemic**, Milos Arhipelago / terra typica in Greece	Rept: Lacertidae
1884	*Blanus strauchi*	Bedriaga	Only European population, Islands of southeastern Aegean Sea	Rept: Amphisbaenidae
1886	*Lacerta trilineata*	Bedriaga	Throughout the country / terra typica in Greece	Rept: Lacertidae
1889	*Pelobates syriacus*	Boettger	Localities in northern Greece and Peloponnese, Lesvos island	Amph: Pelobatidae
1891	*Lyciasalamandra luschani*	Steindachner	Only European population, Kastellorizo island	Amph: Salamandridae
1891	*Rana graeca*	Boulenger	Mainland Greece	Amph: Ranidae
1894	*Anguis cephallonicus*	Werner	**Endemic**, Peloponnese, Ithaca, Cephalonia and Zakynthos islands	Rept: Anguidae
1900	*Anatololacerta anatolica*	Werner	Only European population, Samos island / terra typica in Greece	Rept: Lacertidae
1904	*Anatololacerta oertzeni*	Werner	Only European population, Ikaria, Symi and Rhodes islands / terra typica in Greece	Rept: Lacertidae
1930	*Podarcis gaigeae*	Werner	**Endemic**, Skyros Arhipelago / terra typica in Greece	Rept: Lacertidae
1935	*Macrovipera schweizeri*	Werner	**Endemic**, Milos Archipelago and Siphnos island / terra typica in Greece	Rept: Viperidae
1940	*Pelophylax kurtmuelleri*	Gayda	Mainland Greece, Thassos and Zakynthos islands, most Cycladic islands	Amph: Ranidae
1963	*Lyciasalamandra helverseni*	Pieper	**Endemic**, Karpathos, Kassos and Saria islands / terra typica in Greece	Amph: Salamandridae
1984	*Pelophylax epeiroticus*	Schneider, Sofianidou & Kyriakopoulou- Sklavounou	Western mainland Greece	Amph: Ranidae
1994	*Pelophylax cerigensis*	Beerli, Hotz,	**Endemic**, Karpathos and Tunner, Heppich	Amph: Ranidae Rhodes islands / terra
typica in Greece				
		& Uzzell		
1994	*Pelophylax cretensis*	Beerli, Hotz, Tunner, Heppich & Uzzell	**Endemic**, Crete / terra typica in Greece	Amph: Ranidae
2008	*Podarcis cretensis*	Lymberakis, Poulakakis, Kaliontzopoulou, Mylonas & Valakos	**Endemic**, Crete / terra typica in Greece	Rept: Lacertidae
2008	*Podarcis levendis*	Lymberakis, Poulakakis, Kaliontzopoulou, Mylonas & Valakos	**Endemic**, islets Pori and Lagouvardos close to Antikythira / terra typica in Greece	Rept: Lacertidae

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The history of reptiles and amphibians at Frankfurt Zoo

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Abstract. Reptiles and amphibians were kept in Frankfurt Zoo from the very beginning in 1858. Information on the collection is somewhat fragmentary but still sufficient to draw a picture on its development from then until today. Starting with just a few reptile cages in the monkey house, reptiles soon became a major attraction for the visitors, and a special section in the aquarium building was opened for them in 1904. Knowledge about how to keep reptiles and amphibians was still very poor, but evolved steadily, and shortly before World War II Frankfurt Zoo was famous for its impressive collection of herps, especially crocodilians. Completely destroyed in 1944, the zoo re-opened only a few months after the end of war, but it was not until 1957 that the reptile hall on top of the newly erected aquarium building, which now was called "Exotarium", could be opened. Having undergone a number of improvements and renovations in the last four decades, the Frankfurt Exotarium today has a number of remarkable breeding results and is putting – as the whole zoo – a focus on nature conservation.

Key words: Exotarium, terrarium, herpetological collection, breeding success, nature conservation

THE START WITH A FEW SPECIES

Frankfurt Zoo was opened on 8 August 1858, the second zoo in Germany after Berlin's. Reptiles and amphibians were exhibited here from the beginning. They were shown in a wing of the monkey house and consisted mainly of European species. The first Frankfurt Zoo guide published in 1860 mentions a few tailed amphibians and lizards, snakes and turtles (see Table 1). That chapter on herps also mentions that there were plans to replace the small "reptiles cage" and aquarium by a bigger facility. The newts and the salamanders were at that time kept in the aquarium together with the Great Loach (*Cobitis fossilis*). With regard to the salamanders, it was stated that the animals could be found "on the leaves" in the aquarium, but it is not clear what this means exactly. Were they presented on leaves floating on the water surface?

Unfortunately, aside from this first small "inventory" of the reptiles and amphibians kept in Frankfurt Zoo, a systematic list was started only in the 1950s. Daily reports contained information on new acquisitions, deaths and births, and an electronic register for herps has been started only recently. So there is no detailed, continuous documentation of the herpetological species kept here from the beginning until today. Substantial information on reptiles and amphibians in the Frankfurt collection is scattered over a wide range of articles, zoo guides, and annual reports, allowing one to gain an overall picture with limited, but nevertheless interesting data.

Despite the growing importance and attractiveness of Frankfurt Zoo's herpetological section, not much attention was paid to it in the zoo publications, as will also be shown later. For example, the book published on the occasion of the 100th anniversary of Frankfurt Zoo (Zoologischer Garten der Stadt Frankfurt am Main 1958) has no picture of a reptile or amphibian and only one – rather unimportant – view of the interior of the reptile building from 1957–58.

THE FOUNDING OF THE "DEFINITIVE" ZOO

This first zoo was a huge success as it awoke much interest among the citizens of Frankfurt, but the terrain at the "Leers'scher Garten" was small and could be rented for only ten years. As a consequence, the founders of the zoo decided to find a new location for a bigger and "definitive" zoo. In 1865, the Frankfurt Zoological Society and the Senate of the City of Frankfurt signed a contract to establish a new Zoo at the "Pfingstweide", (then) outside

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Table 1. Herpetological species as mentioned in the first guide to Frankfurt Zoo (Weinland 1860).

Scientific name*	Common name (translated from German)	Remarks (translated from German)
Lacerta viridis	European green lizard	our specimens come from Vienna
Pseudopus Pallasii (scheltopusik, horned serpent)	Glass snake	
Tropidonotus natrix var. *bilineata*	Ringed snake	
Coronella laevis	Smooth snake	
Testudo graeca	Greek tortoise	eats grass, outside during the summer
Testudo polyphemus	Gopher tortoise	on the flamingo meadow during the summer
Triton cristatus, igneus, taeniatus	Our German water salamanders	
Salamandra maculata	Common European salamander	on the leaves

* Note: Scientific names in the whole article, when in quotes, and in this table are given as they are mentioned in the respective publication and have not been transferred into modern nomenclature.

the City of Frankfurt. Reptiles and fishes had turned out to be a real attraction for the visitors, and so, from the beginning, the plan for the new zoo included designs for a herpetological exhibition and aquaria. Due to a number of complications and especially as a consequence of the wars between Prussia and Austria (1866) and France and Germany (1870–71), this contract never materialized and the zoo remained – with an extension of the old contract – at the "Leers'scher Garten" for a few more years. Finally, under a new contract, the new zoo was opened at the Pfingstweide on 29 March 1874, at the same place that had already been envisaged before the wars. Frankfurt Zoo has remained at this site until today. Thanks to an initiative of Bernhard Grzimek immediately after the Second World War it was enlarged and now covers eleven hectares. The city of Frankfurt has grown around it, so today Frankfurt Zoo is in a central location.

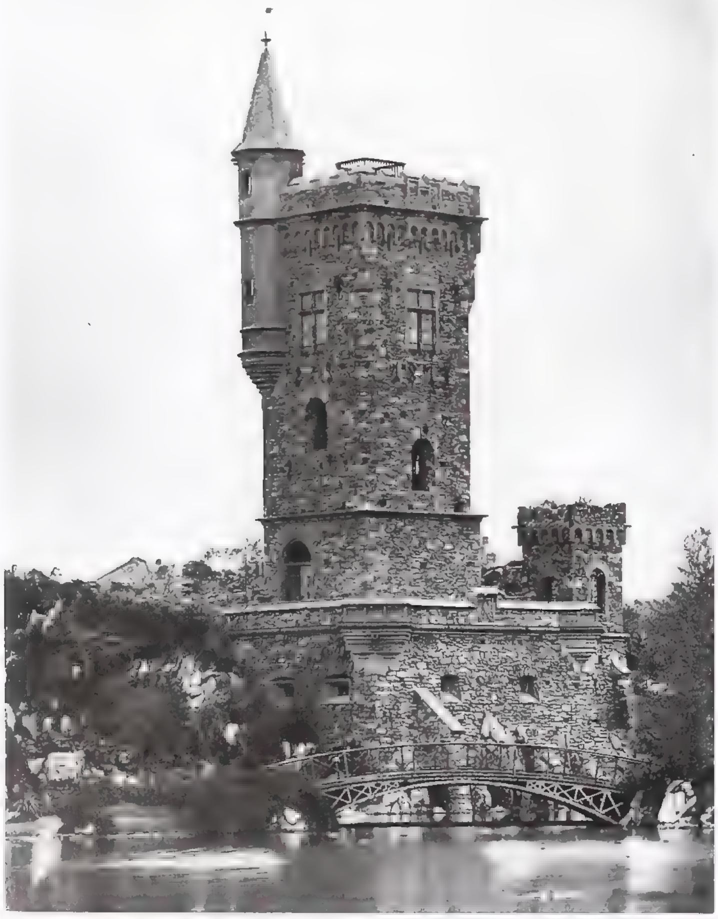

Fig. 1. The „romantic" Aquarium tower of Frankfurt Zoo above the lake in 1880.

SLOW START FOR THE TERRARIUM SECTION

Despite all the plans and good intentions, the construction of a number of enclosures for mammals and birds and, in particular, a new aquarium and terrarium building had to be postponed due to financial and other constraints once the zoo had moved to its new destination in 1874. But at least there was substantial planning, and the knowledge about how to keep fish and herps as well as the development of technical means was rapidly increasing right throughout that period. This is also indicated by the fast growing number of associations of aquarium and terrarium hobbyists in Germany in the last two decades of the 19th century.

To provide the financial means for the aquarium building, the members of the administrative council and supervisory board provided a loan of 50,000 Reichsmarks. In 1877, the building, comprising two freshwater and 12 seawater aquaria and (as far as is known) a few terraria was

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finally able to be opened. The building was placed inside an artificial hill, so the walls were insulated and the temperature could be kept relatively constant. The issue of major concern and of utmost importance for the aquarium section, namely water, was solved by erecting a tower with water tanks inside filled with ground water. This simple technique, based on gravity, is still functioning today, guaranteeing the constant and uniform flow of water into the filters and aquaria.

The tower was made to look like an old castle or ruin, and, together with the hill it stands on and the neighbouring lake, it catered nicely to the romantic taste of that time (Fig. 1).

An extra entrance fee was charged for the aquarium in order to pay the loan back. So the aquarium had its own entrance fee, and only in 1992 was this practice abandoned and no extra fee was charged any more for visiting the aquarium.

DIFFICULT TIMES, BUT A STEADY INCREASE IN EXPERIENCE

The herpetological section had been planned as the second storey of the aquarium building and could only be built later. It finally opened on 15 May 1904. In the ten years before that, the reptiles seem to have had a rather difficult life at Frankfurt Zoo. Especially in winter, many of these animals died because of the poor conditions they were kept in. It was Wilhelm Haacke, director of the zoo from 1888 to 1893, in particular, who expanded the reptile collection. During the summer months, when the monkeys were kept in outside enclosures, he used the monkey house to put boxes with reptiles and amphibians on exhibit. As can be read in the 1895 zoo guide, the "collection that was outstanding because of its richness … [was] usually set up in May, temperatures allowing, and remained there until October, a few boxes (containing the giant snakes and bigger lizards) even remaining on show during the winter". For that latter purpose, a heated platform ("Wärmetisch") had been built in 1891.

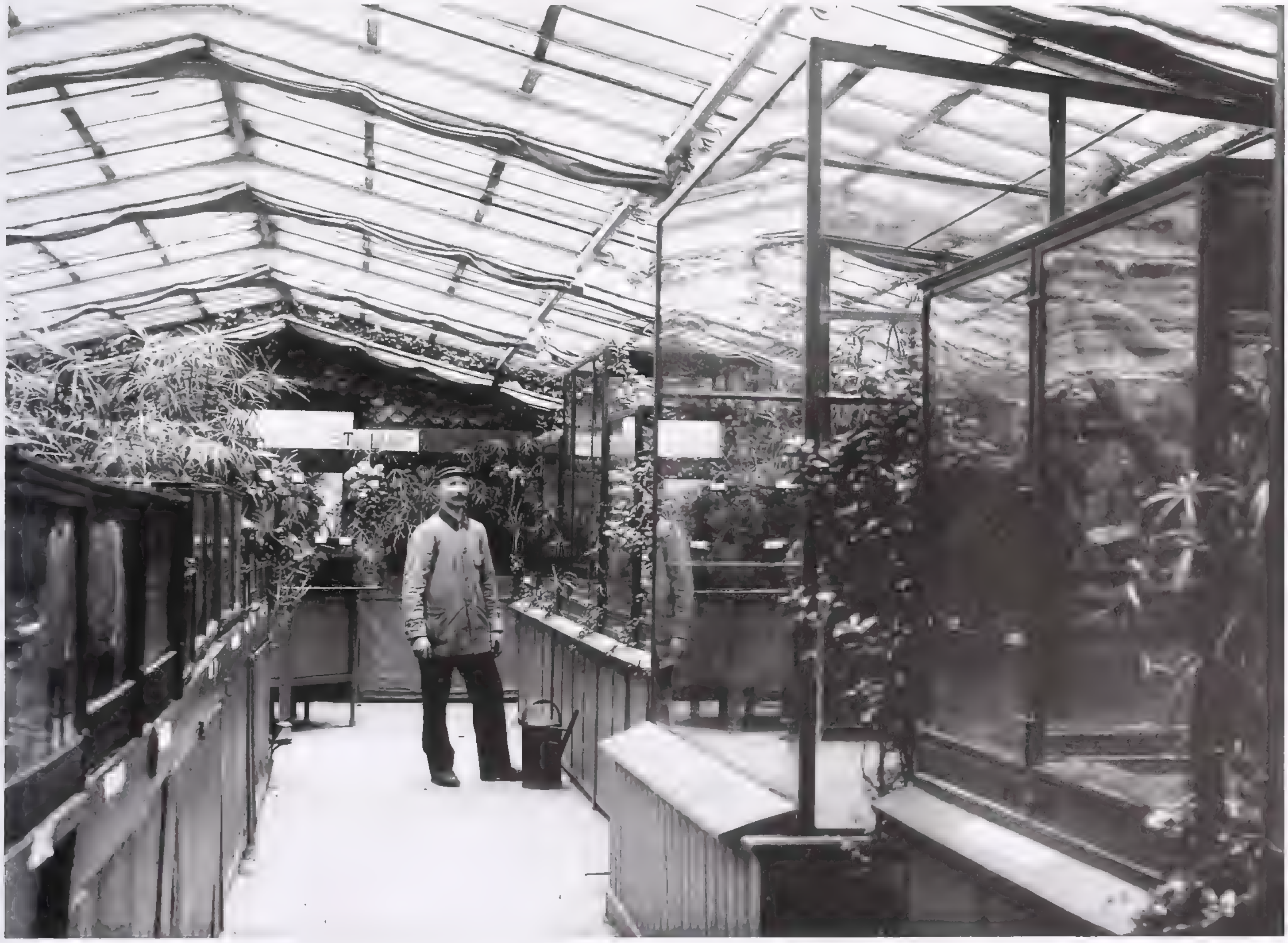

Fig. 2. In the newly opened "Reptile Hall" sunlight was seen an important factor for the well being of reptiles (1904).

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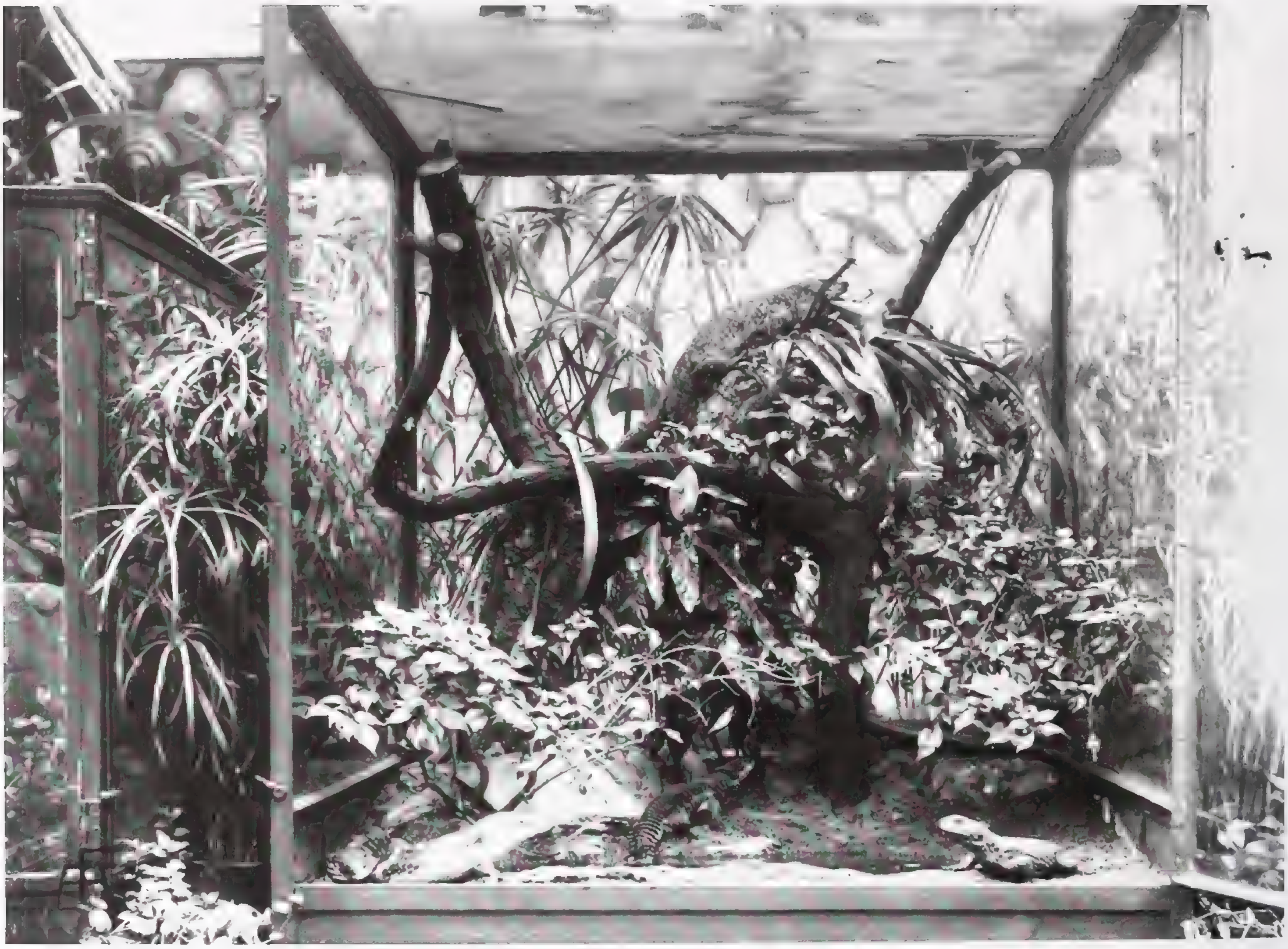

Fig. 3. Mixed life in a tropical jungle environment: *Tiliqua rugosa* (?), *Cordylus giganteus* and *Macroscincus coctei* (1912).

It is plain that mortality was high. The 1895 zoo guide (the first to be published after ten years!) lists, however, an impressive number of species – or to be more precise: two crocodiles, eleven turtles, 17 snakes, 22 lizards and ten anuran species and three species of urodela. A few of the comments and specimens are truly remarkable. So "thanks to the goodness of Mr Schmacker from Shanghai", the collection contained "the first specimen of the Chinese alligator brought live to Europe" and "two giant Aldabra turtles (*Testudo elephantina*)". With regard to the latter, the 1895 zoo guide states that "only a few decades will pass until this turtle of such incredible dimensions will have become extinct". "One of the rarest species at the Zoological Garden, the snake-necked turtle, *Hydraspis hilairei*", was kept together with *Chelydra serpentina*. "The Sinai lizard (*Uromastix ornatus*)" is described as a "very strange animal. It feeds on rose petals in summer and on acacia and lettuce in winter; as soon as the sun shines on its back, it opens certain depressions in the skin and the body assumes a very beautiful colour". The lizard species ranged from *Anguis fragilis* to "*Silubosaurus stokesi*" and from "*Lacerta muralis"* to "*Tiliqua gigas"*. Aside from alpine salamander, Japanese giant salamander, bull frog and *Leptodactylus*, all amphibians kept at that time were species that occurred wild in the Frankfurt area.

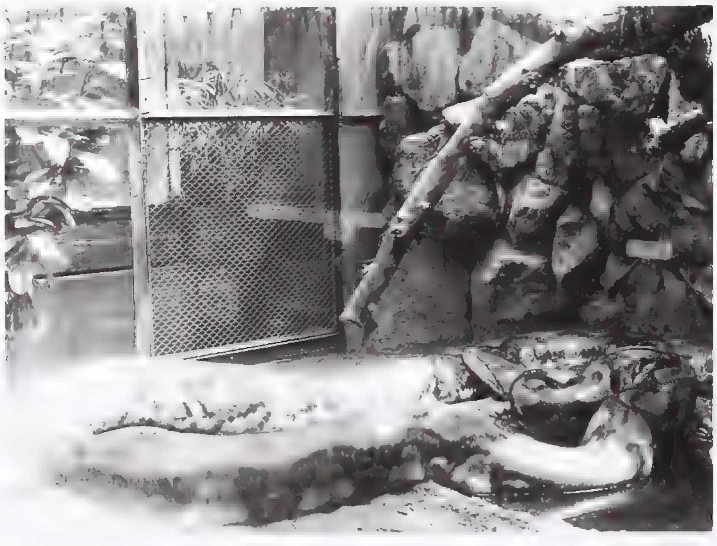

Fig. 4. A big specimen of *Python reticulatus* in its terrarium (1912).

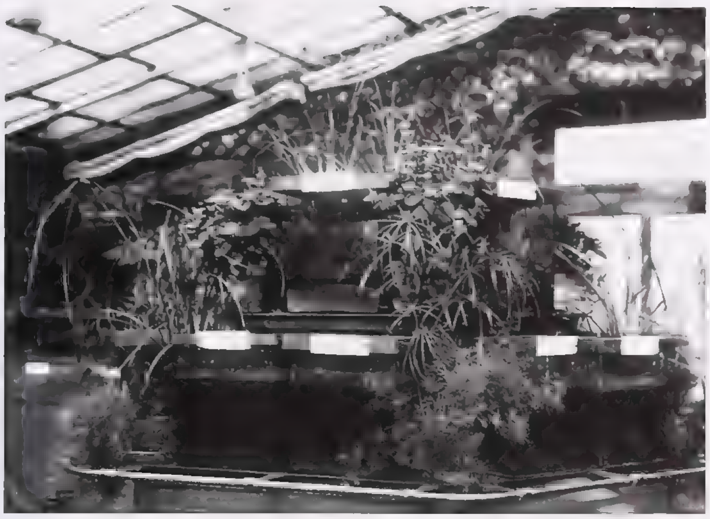

Fig. 5. Tropical jungle landscape made of aquaria and plants (1912).

Haake (who by the way had been vividly recommended by Ernst Haeckel for the post of zoo director) had a well-developed collector's mentality but his attempt to establish systematic collections of birds and herps did not receive much of a positive response from visitors to the zoo, and he quit the job in 1893. His immediate successor, Adalbert Seitz, then started to develop a completely new concept for a reptile exhibit, recognizing that these animals needed sunlight. A glasshouse called the "reptile hall" was erected on top of the aquarium building and inaugurated on 15 May 1904 (Fig. 2). In the venomous snakes section, increased security measures were introduced in the year 1906 to offer the keepers better protection. The number of species had by then risen to twelve turtles, 28 snakes, 25 lizards and 13 amphibians. Evidently there was some "fluctuation" in the crocodile species, as the 1905 zoo guide states: "Mostly different species such as the alligator, Nile crocodile, dwarf crocodile etc. are on exhibit". The *Chlamydosaurus kingi* kept in the collection is said to be the first specimen "to have reached the European continent alive". In 1907, even before becoming zoo director in 1908, the then zoo assistant, Kurt Priemel, started changing the concept again. He wanted to show the visitors the diversity of life, abandoning the approach of systematic collections. He built a second glasshouse next to the first one, added to the reptile hall 40 aquaria for tropical fish (Fig. 5) and a tropical wetland area for crocodiles as well as big terraria for giant snakes (Fig. 4) and turned the reptile house, together with the aquarium, into the "biggest and most diverse of all such institutions on the continent" (Scherpner 1983). As visitors to the zoo had to pay an additional entrance fee for the aquarium and terrarium building, visitor numbers could be easily monitored. The new and enlarged building attracted more than 80,000 people every year.

The zoo did not suffer any major physical damage during the First World War, but the economically difficult post-war era obliged director Priemel to be creative. He made an interesting contract with the animal catcher and dealer John Hagenbeck. Frankfurt hosted reptiles imported by Hagenbeck and, in exchange, got the pre-emption rights and a reduced price on the specimens Priemel wanted to buy. It is reported that visitors were quite astonished by a sign saying "for sale" on a big container full of giant snakes which "none of the visitors managed to count" (Scherpner 1983).

Soon the reptile collection had reached an impressive dimension, and its increasing importance is also documented by a number of articles on it which were published in the Zoo's own "Mitteilungen aus dem Frankfurter Zoo" and elsewhere. One of the authors is Robert Mertens who did evidently have a close relationship with the zoo, since he authored seven papers between 1921 and 1925 specifically about the species and specimens kept at Frankfurt Zoo, and more precisely on the freshwater turtles (1921), giant snakes (1921, 1924 – the latter one not mentioned by Schirner 1977), venomous snakes (1925), news from the reptile house (1922), new animals (1922) and on *Ceratophrys ornata* (1922). An exhaustive paper on the whole collection of reptiles by Richard Wieschke (1925) gives, like the articles just mentioned, short notes and comments on the different species shown and mentions, as a special attraction, a giant salamander from Japan which was exhibited in an aquarium in the lower basement. From that description of the collection one can deduce that, in 1925, there were more than 40 snake species, 28 lizard species, more than 20 turtles and tortoises (including a loggerhead sea turtle), and seven crocodile species on exhibit. An interesting detail is the mentioning of a female reticulated python 8 m in length which, after having undergone "difficult surgery", had not taken any food for 16 months before she finally accepted a piglet. Six anuran and 2 urodelan species are specifically mentioned as part of the collection "plus the numerous European frogs, toads, salamanders and newts". Among the amphibians mentioned are "two giant bull frogs…, and, even more impressive, two South American horned frogs", as well as African clawed frogs "which because of their hopping movements under water soon got the name 'water monkeys'", besides *Pipas*, a Japanese giant salamander and a *Proteus*.

Whereas Robert Mertens is well known among herpetologists even today and does not need to be introduced to the reader, a few words have to be said about Wieschke. In one of the articles, his name is given as "Fritz", in the other article as "Rich[ard]". It was not possible to find out if Fritz and Rich[ard] Wieschke were the same person – and "Fritz" a printing error? – or whether and how they

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were related. "Fritz" could not be identified at all, whereas it is known that Richard was a volunteer assistant, helping out quite actively with many activities in the zoo such as the administration of the library, keeping the register of animals and observing them. He published several small papers in the Mitteilungen, the last one appearing in November 1928, and, as far as is known, died at the age of 23 in 1929.

A remark in a review authored by zoo director Priemel on issues 1 and 2 of Wilhelm Klingelhöffer's Terrarienkunde in the Mitteilungen from May 1925 gives an interesting insight into the concept of reptile keeping. Priemel welcomes Klingelhöffer's approach to arranging the contents of the terraria in such a way that they resemble the habitat of the species in the wild. Furthermore, he writes that terraria for schools should always be arranged so that they imitate nature, but then he goes on to write: "Unfortunately, the containers in public exhibitions cannot follow this principle, as so many inhabitants must be kept in them in order that visitors can observe the major part of them at any time of the day".

In the following years, the collection continued to grow and attracted more and more visitors. Various publications talk about anacondas, chameleons, Gila monsters and sea turtles all becoming part of the collection and, of course, about "Komo", the tame Komodo monitor lizard which came to Frankfurt in 1927, only 15 years after this species had been discovered. It was brought from Komodo to Frankfurt by Robert Mertens. Frankfurt already had some experience in taming monitor lizards. Two *Varanus salvator* had come to Frankfurt Zoo in 1922–23, when they were just 25 cm long. They were quite aggressive and, while one died, the other one had grown to a length of 1.35 m by 1926 and thanks to "persistent, gentle, careful treatment and care" had become tame. Whenever the door to his enclosure was opened or his name ("Bubchen", little boy) was called, he climbed onto the keeper's shoulder and allowed himself to be carried around (Fig. 7).

In that time before World War II, discussions arose about the rights and wrongs and justifications of keeping animals "in captivity", and, as one of the arguments in favour of zoos, curator Gustav Lederer (1937) published information about the longevity of reptiles at Frankfurt Zoo.

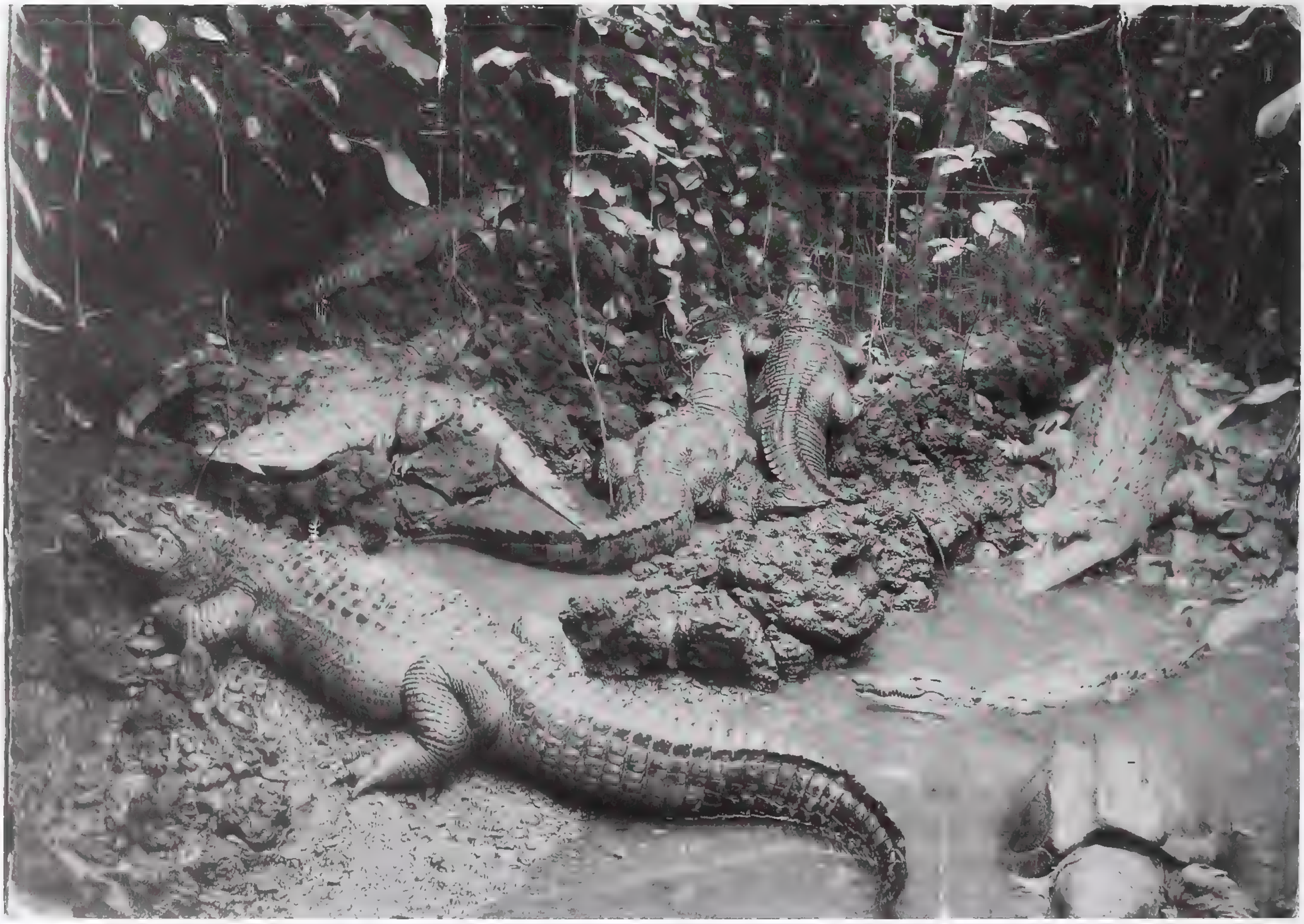

Fig. 6. Different species, different sizes: A look into the "world renown" crocodile collection in 1925. Note the *Macroclemys* in the right foreground.

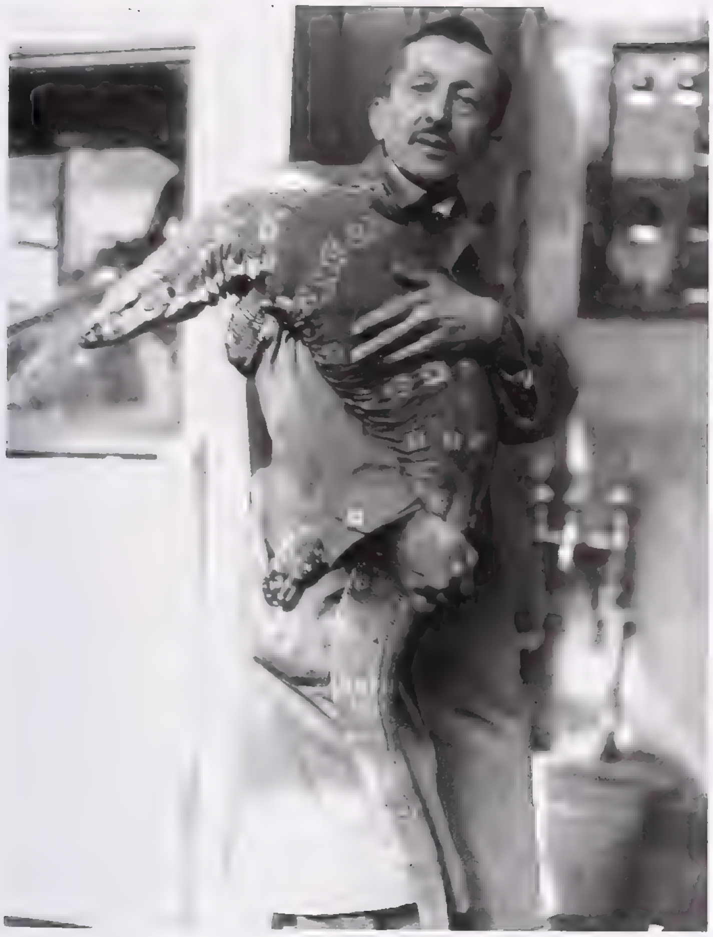

Fig. 7. *Varauns salvator* "Bubchen" and his keeper – in the truest sense of the word! – in 1929.

In that year, the zoo was home to an *Alligator mississippiensis,* a *Trionyx triunguis* and two *Heloderma suspectum* that had been living at the zoo since 1905, 1912 and 1927 respectively, as well as a Chinese alligator. The latter had moved to Frankfurt in 1910 when the Berlin Aquarium had to be closed because of financial problems and Frankfurt took over its entire reptile collection. This alligator had come to the Berlin Aquarium in 1886 and so had lived for 30 years in Frankfurt when he died in 1940.

The already highly diverse collection of crocodiles was enriched by a *Tomistoma schlegeli* in 1937, raising the number of species kept to eight. In addition, young and old, small and large individuals were all kept together (Fig. 6). This crocodile collection is repeatedly referred to as a major attraction and as "world renowned" (Lederer 1937), but, looking at it today, it certainly must be regarded as highly problematic from a zoological point of view as well as from the aspects of animal welfare. Wieschke (1927) mentions, for example, that the "newly created tropical swamp area for crocodiles" is host to "numerous species, among others a large number of American alligators (*Alligator mississippiensis)*, one of the few surviving specimens of the Chinese alligator, Nile crocodiles, saltwater crocodiles and African dwarf crocodiles" – each in the plural! A completely new approach to keeping crocodiles was only introduced around 1975, when this collection was finally dissolved to create a larger crocodile enclosure.

With the retirement of Kurt Priemel in March 1938, the dynamic development of the herp collection came to an end, as his successor, Georg Steinbacher, was more of a "bird man" and evidently not much interested in reptiles. The first bombs hit Frankfurt Zoo in October 1943, causing some limited damage including to the aquarium building, but most, if not all, of the reptiles survived. The venomous snakes, however, now had to be put down for security reasons. A few months later, the disastrous bombing of Frankfurt on 18 March 1944 completely destroyed the zoo and the aquarium with all its animals (Fig. 9).

ON THE WAY TO A MODERN ZOO: THE PERIOD AFTER WORLD WAR II

The reconstruction of the zoo, under its new director Bernhard Grzimek, started immediately after the end of the war. The zoo re-opened on 1 July 1945, offering its visitors a few animals and a lot of entertainment in the form of all kinds of cultural events, circus shows, carousels and so on. The re-building of the aquarium started in 1951 and the shell of a "24 m long tropical swamp area destined for the keeping of crocodiles, turtles and so on" had been completed in 1952. Precisely 1 chameleon, four snakes, 26 turtles and seven crocodiles were housed in the preliminary terraria in 1953. From then on, more and more reptiles and amphibians were acquired by or donated to the zoo. The building with the new big reptile hall was opened officially on 27 August 1957 and by the end of that year, it had had 282,084 visitors. There were "giant crocodiles able to kill a human being" and "gigantic land tortoises 200 years of age" living in the (altogether eleven) "climatic landscapes", with plant arrangements giving the visitor the illusion of being in a tropical jungle.

As the "aquarium" was now housing fish and other aquatic animals, as well as penguins in an Antarctic environment and a few other birds in the tropical section, along with many reptile and amphibian species, it was decided to give it a new name to better reflect the situation and intention of the building. Since 1954, this building has therefore been known as the "Exotarium". The innovative ideas and plans for the Exotarium were basically developed by Gustav Lederer, who had already been the key person for the "pre-war" aquarium under director Priemel. After the war, he became the zoo's chief curator. How farsighted and innovative his thinking was and how carefully he observed his animals is reflected, for example, in his paper on the "importance of light in animal keeping" (Lederer 1927).

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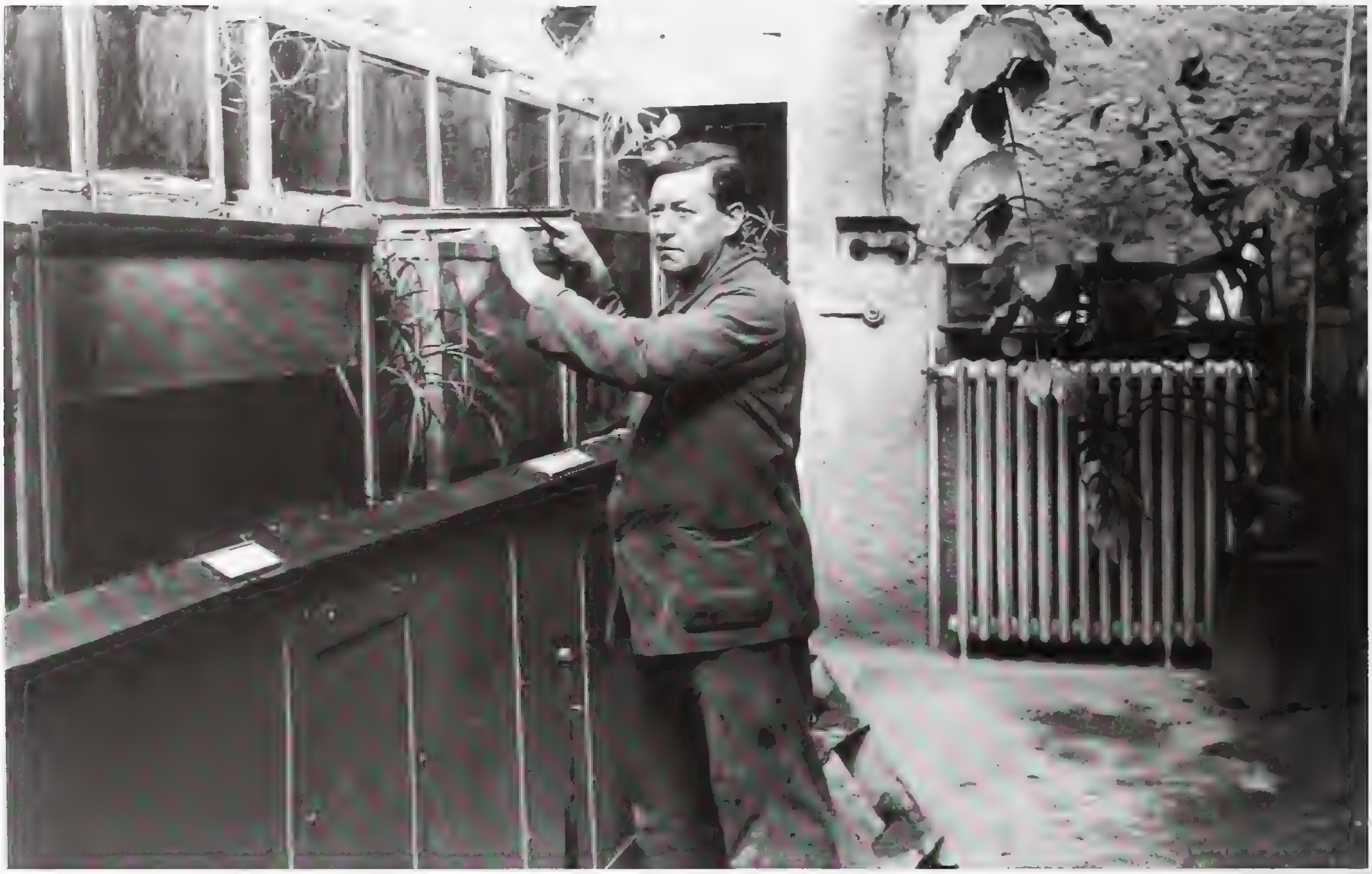

Fig. 8. An unidentified keeper working in the terrarium section (1936).

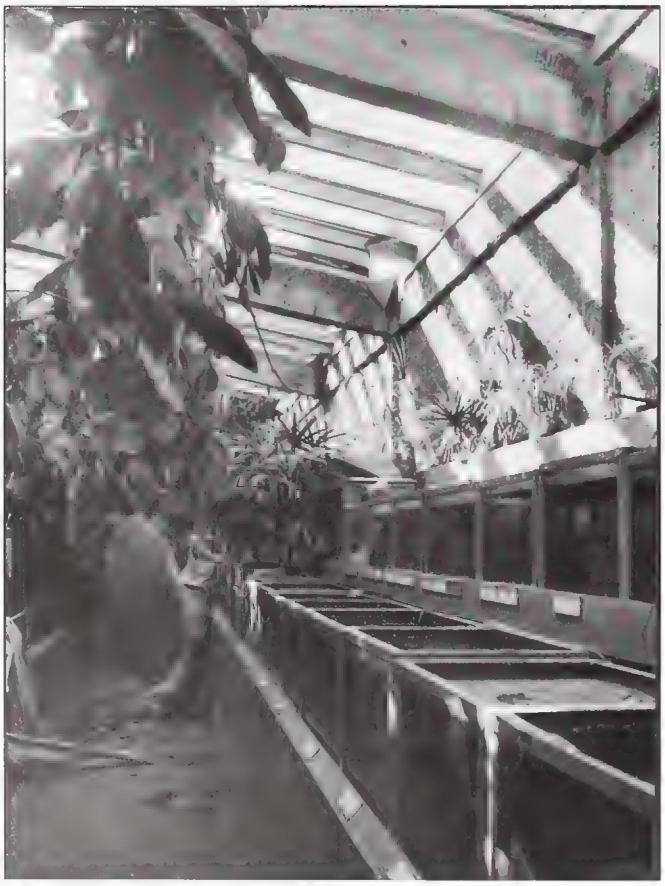

Fig. 9. View of the reptile hall after the bombing in 1944.

At the suggestion of Bernhard Grzimek and in recognition of his merits and the quality of his scientific publications, he received an honorary doctorate from Frankfurt University in 1953. He retired on 30 September 1958, after having served Frankfurt Zoo for 45 years, accompanying it through two world wars and all its ups and downs. Gustav Lederer died at the age of 69 on 13 February 1962.

THE EXOTARIUM TODAY

Despite all changes, improvements and renovation activities in the 1980s and 1990s, the concept of the herpetological section of the Frankfurt Exotarium until today essentially goes back to Gustav Lederer. He was followed by curator Dieter Backhaus who, in 1973, handed over to Hartmut Wilke. It was still a time of much "trial and error", since knowledge regarding the keeping of reptiles was still limited. In 1960, a few adult and juvenile specimens of *Amblyrhynchus cristatus* were even exhibited, but did not survive the first two years.

Reptiles and amphibians were selected for their "didactic, zoogeographical and ecological aspects" and the zoo "dispensed with animals which were always hiding away during opening hours". Backhaus, as well as his succes-

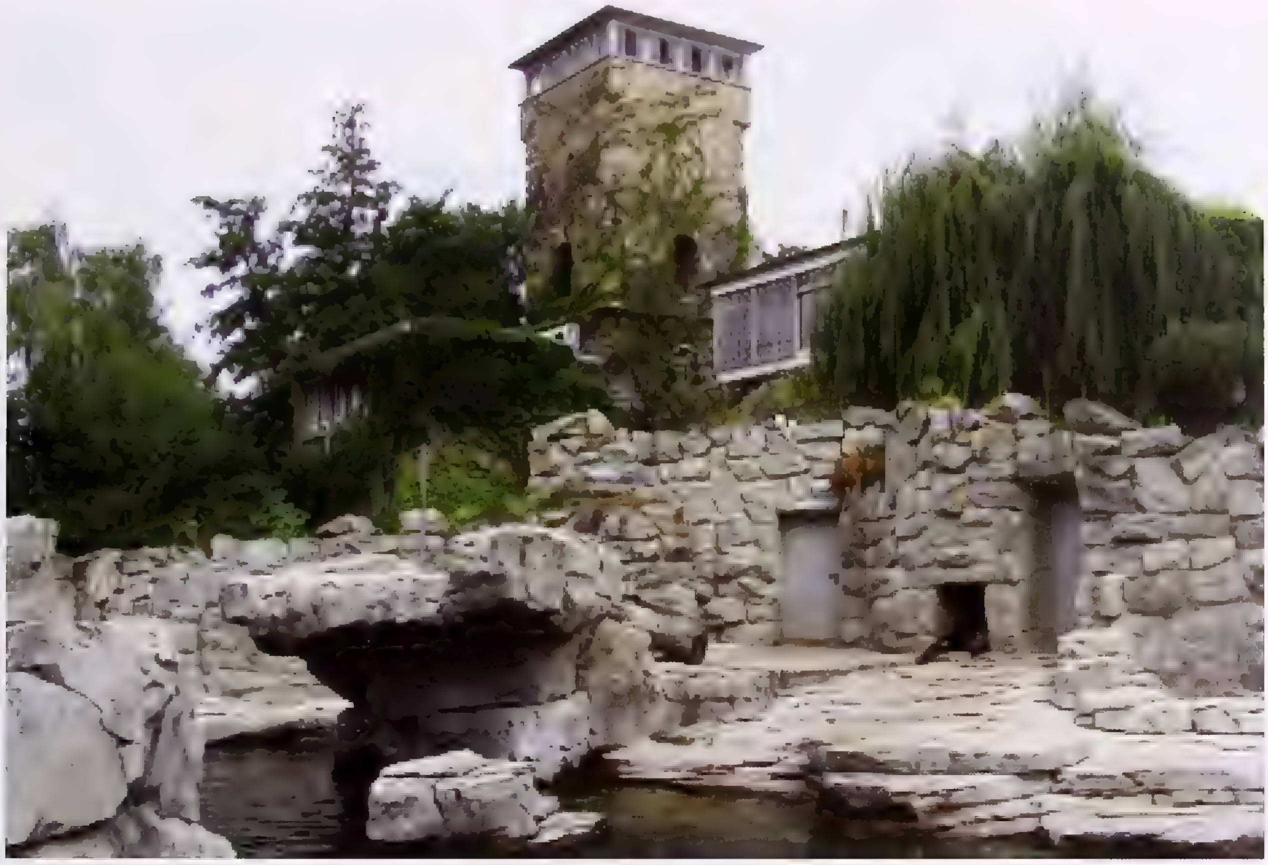

Fig. 10. The Exotarium Tower overlooking the "seal cliffs" (2008). Photograph: Sabine Binger.

sor, constantly tried to improve the living conditions of the animals, trying out all sorts of lamps, heating equipment and other means to improve the climate control of the terraria. They also did lots of work on nutrition and disease prevention and carried out the associated physical changes and improvements to the building, such as special rooms to prepare food, raise foraging animals and raise newly born reptiles and amphibians. Terraria were equipped with appropriate soil substrate for digging species as well as stones and trees for climbing species, in addition to hiding places and other structures, paving the way to modern reptile keeping. Another remarkable change was the renovation of the crocodile enclosure which had made it necessary to give up the crocodile collection in around 1975 and to send the gharial (which had been living at Frankfurt Zoo since 1958) to the Gharial Breeding Centre in Orissa, India in 1979. After the renovation of the building had been completed, Nile crocodiles returned to the zoo in 1977, but the enclosure turned out to be unsuitable for that aggressive species.

Finally, in 1990, Frankfurt Zoo started keeping Australian freshwater crocodiles, which started breeding regularly in 1994 and still do so today. This is one of the many breeding successes at the Frankfurt Exotarium since Rudolf Wicker became its curator in 1984. He took over at a time when again some necessary renovation work had started, and so the opportunity to build a big landscape terrarium for freshwater tortoises (1987) was seized. The group of *Cyclura cornuta* then consisted of shy and aggressive animals. They had come to the zoo in 1974, but Wicker replaced them by ten new animals imported from the zoo in Santo Domingo. These animals laid eggs for the first time in 1987, but the keeping facility was not the most favourable in many aspects, and there was little breeding success. Just a few weeks after they had been moved to a newly built enclosure in 1991, they started breeding successfully and have done so ever since.

Other remarkable breeding successes of the last two decades have been the *Phelsuma klemmeri* from Madagascar, *Varanus salvator cumingi* and *Erymnochelys madagascariensis*, as well as the *Laemanctus serratus* and *Petrosaurus thalassianus* that were all bred in Frankfurt for the first time ever under human care. Our specimens of *Crocodylus johnsoni* form the only breeding group outside Australia, and Frankfurt Zoo keeps and breeds *Ctenosaura bakeri*, the highly endangered iguana from Utila island.

Especially as Frankfurt Zoo has made nature conservation *in situ* and *ex situ* one of its top priorities, its close cooperation with the Customs Service at Frankfurt Airport must also be noted. Every year, this results in hundreds of reptiles being seized from travellers or commercial shipments at Frankfurt Airport and being brought to the Exotarium

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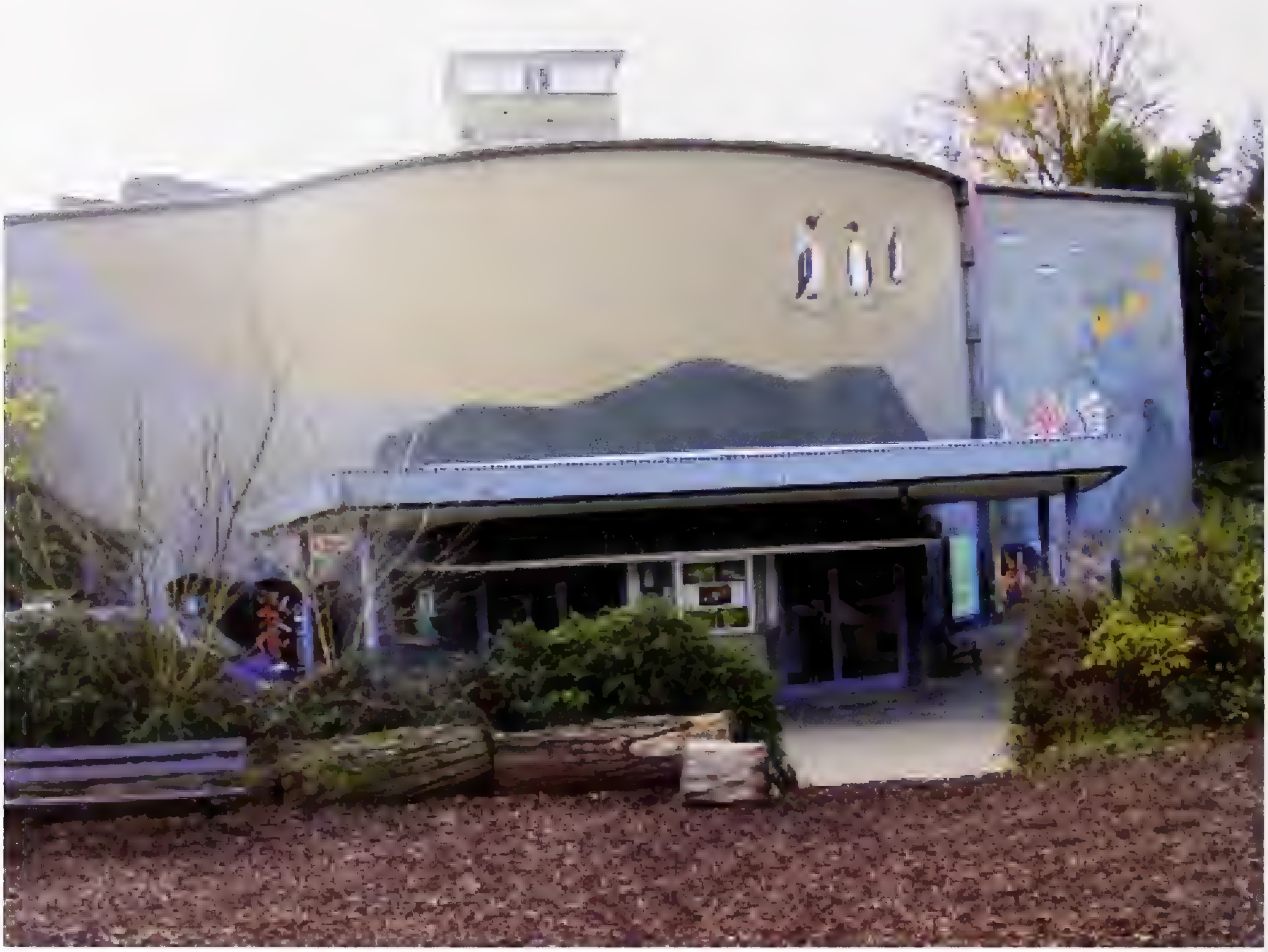

Fig. 11. The entrance to the Frankfurt Exotarium still preserves the charm and character of the 1950s when it was rebuilt (2008). Photograph: Sabine Binger.

– even rare animals such as a few *Psammobates* from two different species. Some of the shipments seized contain quite a number of specimens, for example 300 *Geochelone elegans* or more than 70 *Cordylus mossambicus* and *C. rhodesianus* and, repeatedly, also large numbers of poison arrow frogs. Particularly with regard to the more common species and relatively high numbers of specimens, it is extremely difficult to find appropriate people and institutions willing and able to take them on. All these animals are lost to the natural world as they cannot usually be taken back and released into the wild.

One exception was the case of five hawksbill turtles (*Eretmochelys imbricata*) in 2009. Dogs trained to detect CITES species at Frankfurt Airport discovered the eggs in the luggage of a tourist. The eggs were brought to the Exotarium, and, as they looked good, were put into an incubator. During the following days, the turtles hatched and were kept in an aquarium until they had reached a length of around 20 cm. As it was known from which beach in the Seychelles they had been collected, they could be sent back and were released into the sea by the local authorities. The media attention was huge, and so this successful, but quite untypical, story could be accompanied by the message that one should not take home souvenirs of endangered and protected species.

Generally, species conservation aspects today play an important role in Frankfurt Zoo, and this, of course, also applies to the Exotarium. This building, with its long and interesting history and its rich collection of reptiles and amphibians, is certainly one of the best places in Frankfurt Zoo to demonstrate to the visitors the multitude of forms, colours, adaptations and other expressions of the diversity of life. Today, there is neither a separate entrance fee nor any counting of the number of visitors to the Exotarium, but, in all probability, it may be assumed that almost all the visitors to Frankfurt Zoo (more than 900,000 per year!) also visit the Exotarium. Showing around 170 adult specimens of 29 amphibian species and more than 400 reptiles from 68 species, it is and remains one of the main attractions of Frankfurt Zoo.

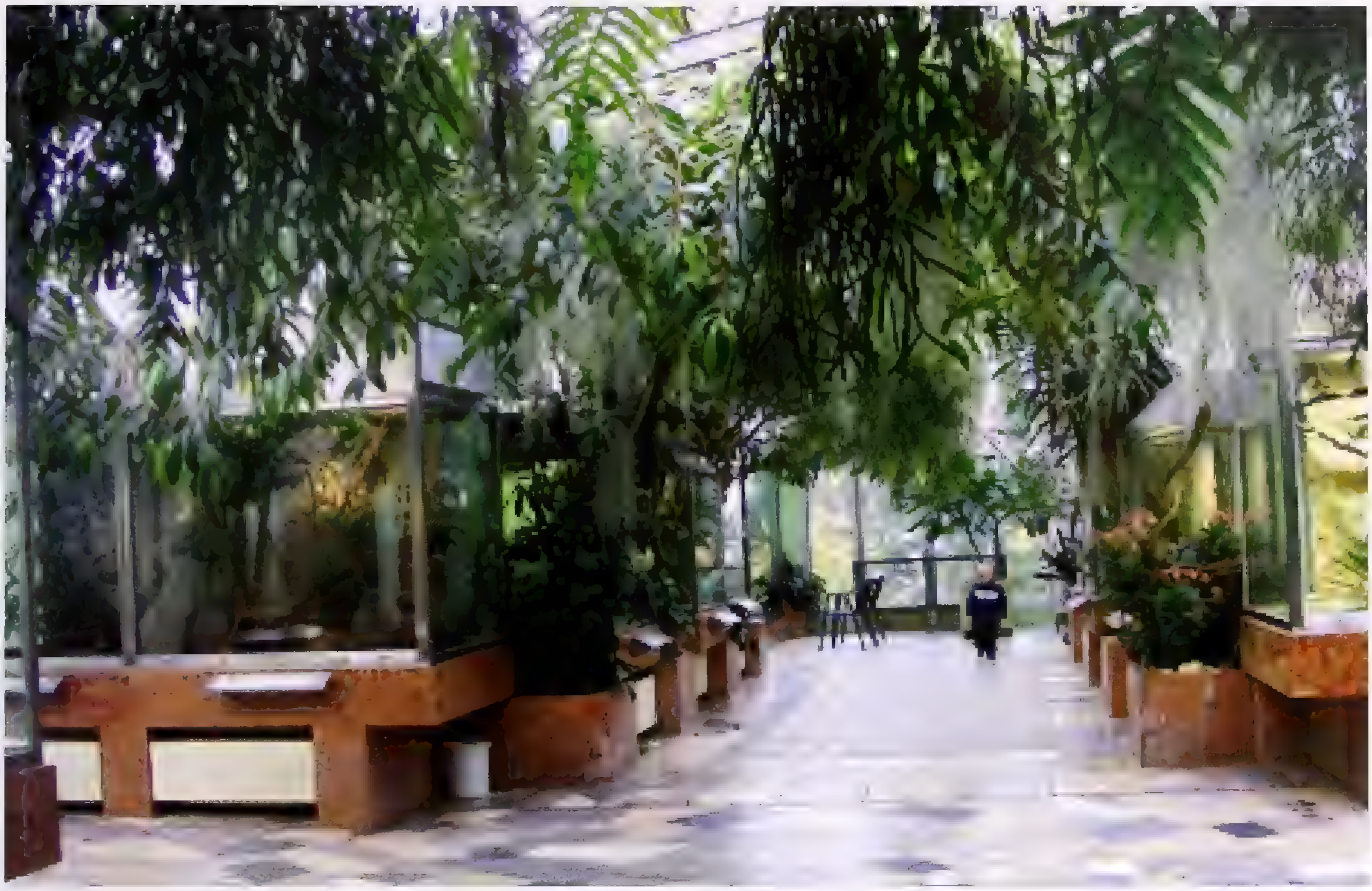

Fig. 12. Despite all changes the Reptile Hall today still resembles in many aspects the one opened in 1904 (2008). Photograph: Sabine Binger.

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Tetramorium boehmei sp. n. – a new ant (Hymenoptera: Formicidae) species from the Kakamega Forest, Western Kenya

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Abstract. *Tetramorium boehmei* Hita Garcia & Fischer sp. n. – a new ant species from the Kakamega Forest in Western Kenya is described. The new species can be placed in the *Tetramorium camerunense* species group and differs significantly from the other members of the group by its highly reduced sculpturation on head and mesosoma. With only two available specimens sampled in undisturbed primary forest, *Tetramorium boehmei* sp. n. seems to be a relatively rare endemic species. Additionally, a first key to the *Tetramorium* species groups found in the Kakamega Forest is provided.

Keywords. Ants, Kakamega Forest, species group key, taxonomy, *Tetramorium*, *Tetramorium camerunense* species group.

INTRODUCTION

The ant genus *Tetramorium* Mayr, 1855 is almost globally distributed, and with over 430 described species one of the most species-rich genera worldwide (Bolton 1995; B Bolton, Isle of Wight, pers. comm. 2010). The Afrotropical zoogeographic region holds the largest diversity with over 210 listed *Tetramorium* species (Bolton 1976, 1980, 1985, 1995; Hita Garcia et al. 2010).

The Kakamega Forest, one of the last indigenous forests in Kenya, and its animal diversity have received considerable scientific attention in the last decades (e.g. Clausnitzer 1999, 2005; Copeland et al. 2005; Hita Garcia et al. 2009; Kühne 2008; Schick et al. 2005; Tattersfield et al. 2001; Wagner & Böhme 2007; Zimmermann 1972). Generally, the forest is considered to be the eastern-most relict of the equatorial Guineo-Congolian lowland rain forest belt (Kokwaro 1988; Wagner et al. 2008; Zimmermann 1972). The strong biogeographic affinities to West and Central African forests can be clearly seen in some faunal elements like reptiles, dragonflies, and ants (Clausnitzer 2005; Hita Garcia et al. 2009; Wagner et al. 2008). The ant fauna proved to be remarkably diverse with 288 species from 52 genera and 11 subfamilies constituting the second highest species richness reported for the Afrotropical zoogeographic region (Hita Garcia et al. 2009). By far the most species-rich genus in Kakamega Forest was *Tetramorium* with more than 40 species belonging to 14 species groups (Hita Garcia et al. 2009; FHG, unpublished). The *Tetramorium camerunense* species group was well represented with four species: *Tetramorium lucayanum* Wheeler, W.M., 1905, *Tetramorium* cf. *gegaimi* Forel, 1916, and two undescribed species.

Recent taxonomic work was primarily focused on the *Tetramorium weitzeckeri* species group with the description of *Tetramorium snellingi* Hita Garcia, Fischer & Peters, 2010 and a species group revision for the whole Afrotropical region (FHG, unpublished). However, around 10 species or 25% of the *Tetramorium* fauna of the Kakamega Forest still remain undescribed. With this work we present a first preliminary key to the *Tetramorium* species groups present in the Kakamega Forest and describe a new species belonging to the *T. camerunense* species group.

MATERIAL AND METHODS

The type material has been deposited in the following institutions:

NMK: National Museums of Kenya, Nairobi, Kenya
ZFMK: Zoological Research Museum Koenig, Bonn, Germany

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Both, holotype and paratype, were measured with an Olympus SZX 12 stereomicroscope equipped with a dual-axis optical micrometer at a magnification of 90x. The following measurements and indices, in parts adapted from Bolton (1980) and Güsten et al. (2006), were used:

Head length (HL): maximum distance from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin, measured in full-face view.

Head width (HW): width of head directly behind the eyes measured in full-face view.

Scape length (SL): maximum scape length excluding basal condyle and neck.

Eye length (EL): maximum diameter of compound eye measured in oblique lateral view.

Pronotal width (PW): maximum width of pronotum measured in dorsal view.

Weber's length (WL): diagonal length of mesosoma in lateral view from the postero-ventral margin of propodeal lobe to the anterior-most point of pronotal slope, excluding the neck.

Propodeal spine length (PSL): in dorsocaudad view, the tip of the measured spine, its base, and the centre of the propodeal concavity between the spines must all be in focus. Using a dual-axis micrometer the spine length is measured from the tip of the spine to a virtual point at its base where the spine axis meets orthogonally with a line leading to the median point of the concavity.

Petiole length (PTL): maximum length of petiolar node measured in dorsal view.

Petiole height (PTH): maximum height of petiolar node measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed in an orthogonal angle to the ventral outline of the node.

Petiole width (PTW): maximum width of petiolar node measured in dorsal view.

Postpetiole length (PPL): maximum length of postpetiole measured in dorsal view.

Postpetiole height (PPH): maximum height of the postpetiole measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed in an orthogonal angle to the ventral outline of the node.

Postpetiole width (PPW): maximum width of postpetiole measured in dorsal view.

Ocular index (OI): EL / HW * 100
Cephalic index (CI): HW / HL * 100
Scape index (SI): SL / HW * 100
Propodeal spine index (PSLI): PSL / HL * 100
Petiolar node index (PeNI): PTW / PW * 100
Lateral petiole index (LPeI): PTL / PTH * 100
Dorsal petiole index (DPeI): PTW / PTL * 100
Postpetiolar node index (PpNI): PTW / PW * 100
Lateral postpetiole index (LPpI): PPL / PPH * 100
Dorsal postpetiole index (DPpI): PPW / PPL * 100
Postpetiole index (PPI): PPW / PTW * 100

Measurements and indices are presented as minimum and maximum values. Additionally, all measurements are expressed in mm and presented with three decimal places.

The digital colour images were produced with a QImaging Micropublisher 5.0 RTV camera attached on a LEICA Z6 APO stereo-microscope and mounted with Syncroscopy Auto-Montage software (version 5.03). The mounted images were processed for publication with Adobe Photoshop CS2 and ImageJ. All images presented in this work are also online available at Antweb (Fisher, 2002). Furthermore, holotype and paratype are uniquely identified with specimen-level codes (e.g. CASENT0217239) affixed to each pin.

Total genomic DNA was extracted from two dissected single legs of the holotype, using the Qiagen DNeasy®Blood&Tissue Kit, following the manufacturers` protocol. DNA was eluted with 50 µl buffer AE; this step was repeated once to maximize yield.

A ca. 650 bp long fragment of the 5´-region of the cytochrome c oxidase subunit I (COI), the standard DNA barcode-marker for animals, was amplified using the primers LCO 1490 and Nancy (5´-GGT CAA CAA ATC ATA AAG ATA TTG G-3´ and 5´-CCC GGT AAA ATT AAA ATA TAA ACT TC -3´; Folmer et al. 1994) and the Qiagen® Multiplex PCR Kit. Amplification reactions were carried out in a 20 µl volume containing 10 µl QIAGEN Multiplex PCR Mastermix, 2 µl Q-Solution, 1.6 µl of each primer (both 10 pmol/µl), and 2.5 µl DNA template, and filled up to 20 µl with sterile H_2O. The PCR temperature profile consisted of an initial denaturation at 95° (15 min), followed by 40 cycles at 94° (35 s, denaturation), 48.5° (90 s, annealing), 72° (90 s, extension), and a final extension at 72° (10 min). PCR success was checked by electrophoresis on an 1.5% agarose gel containing ethidium bromide. The PCR product was purified using 3 µl of the ExoSAP-IT® PCR purification reagent following the manufacturers` protocol.

The sample was bidirectionally sequenced by a commercial company (Macrogen Inc., Seoul, Republic of Korea; http://www.macrogen.com) using PCR primers. BLAST search confirmed belonging of the sequence to the genus *Tetramorium*. The sequence is deposited in GenBank (accession number HM753586).

KEY TO THE *TETRAMORIUM* SPECIES GROUPS FOUND IN KAKAMEGA

The following key to species groups is adapted from Bolton (1976, 1980) and specific for the Kakamega Forest, though it also works for Western Kenya in general:

1 Whole body covered with regularly branched hairs, either bifid or trifid, giving the ant a woolly or furry appearance. **2**
– Hairs generally simple, rarely bizarrely modified, but never regularly branched bifid nor trifid as above . **3**

2 Antennae 11-segmented; elongate simple hairs present along the antennal scapes and upper borders of the frontal carinae. .... *T. ericae* group
– Antennae 12-segmented; elongate simple hairs absent along the antennal scapes and upper borders of the frontal carinae. .... *T. gabonense* group

3 Antennae 11-segmented. **4**
– Antennae 12-segmented. **5**

4 Petiolar node squamiform to high nodiform, never blocky nodiform with sharply defined angles. .... *T. weitzeckeri* group
– Petiolar node strongly blocky nodiform, generally with sharply defined angles. ... *T. angulinode* group

5 Lateral portion of clypeus prominent, raised to a tooth or crest in full-face view; in dorsal view the lateral clypeal portions rise to a high peak in front of the antennal insertions and then slope down towards the median part of the clypeus. .... *T. sericeiventre* group
– Lateral portion of clypeus not modified as above. . **6**

6 Antennal scapes very long (always SI > 120); frontal carinae weakly developed and short, at most reaching the posterior eye margins. .... *T. aculeatum* group
– Antennal scapes distinctly shorter than above (always SI < 110); frontal carinae variable. **7**

7 Propodeum armed with a pair of small triangular teeth or denticles which at most are as large as the propodeallobes. **8**
– Propodeum armed with a pair of medium-sized to long spines which are noticeably larger than the propodeallobes. **12**

8 Anterior clypeal margin with median impression. .... *T. dumezi* group (in parts)
– Anterior clypeal margin entire. **9**

9 Tibiae with short appressed pubescence. **10**
– Tibiae with subdecumbent to erect pilosity or pubescence. **11**

10 Hairs on dorsal mesosoma and gaster usually sparse, short, stout, and blunted .... *T. simillimum* group
– Hairs on dorsal mesosoma and gaster usually numerous, elongate and fine .... *T. quadridentatum* group

11 Frontal carinae long, usually reaching occiput. .... *T. dumezi* group (in parts)
– Frontal carinae short and weakly developed, ending at eye level. .... *T. convexum* group

12 Anterior clypeal margin with median impression. .. **13**
– Anterior clypeal margin entire, without a median impression. **14**

13 Occipital region of head variably rugose, rugulose or unsculptured, rarely with few anastomoses, without a rugo-reticulum. .... *T. camerunense* group
– Occipital region of head distinctly rugo-reticulate. .... *T. bicarinatum* group

14 Eyes larger, at least 9 ommatidia in the longest row. .... *T. setigerum* group
– Eyes smaller, at most 7 to 8 ommatidia in the longest row. .... *T. flabellum* group

Tetramorium camerunense species group

Examination of the new species led to the conclusion that it can be easily placed in the *T. camerunense* species group. Though the species group was well defined in Bolton (1980) it seems useful to reproduce it here:

1. antennae 12-segmented
2. antennal scape relatively small to moderate (SI < 90)
3. anterior clypeal margin generally with small median impression (absent in one species)
4. frontal carinae long and fine, generally reaching posterior eye margin, sometimes running to occipital margin
5. antennal scrobe weakly developed
6. propodeal spines of varying length, but always longer than propodeal lobes
7. mandibles generally smooth and shining, rarely finely striate
8. clypeus with three longitudinal rugae
9. cephalic dorsum usually finely longitudinally rugu-

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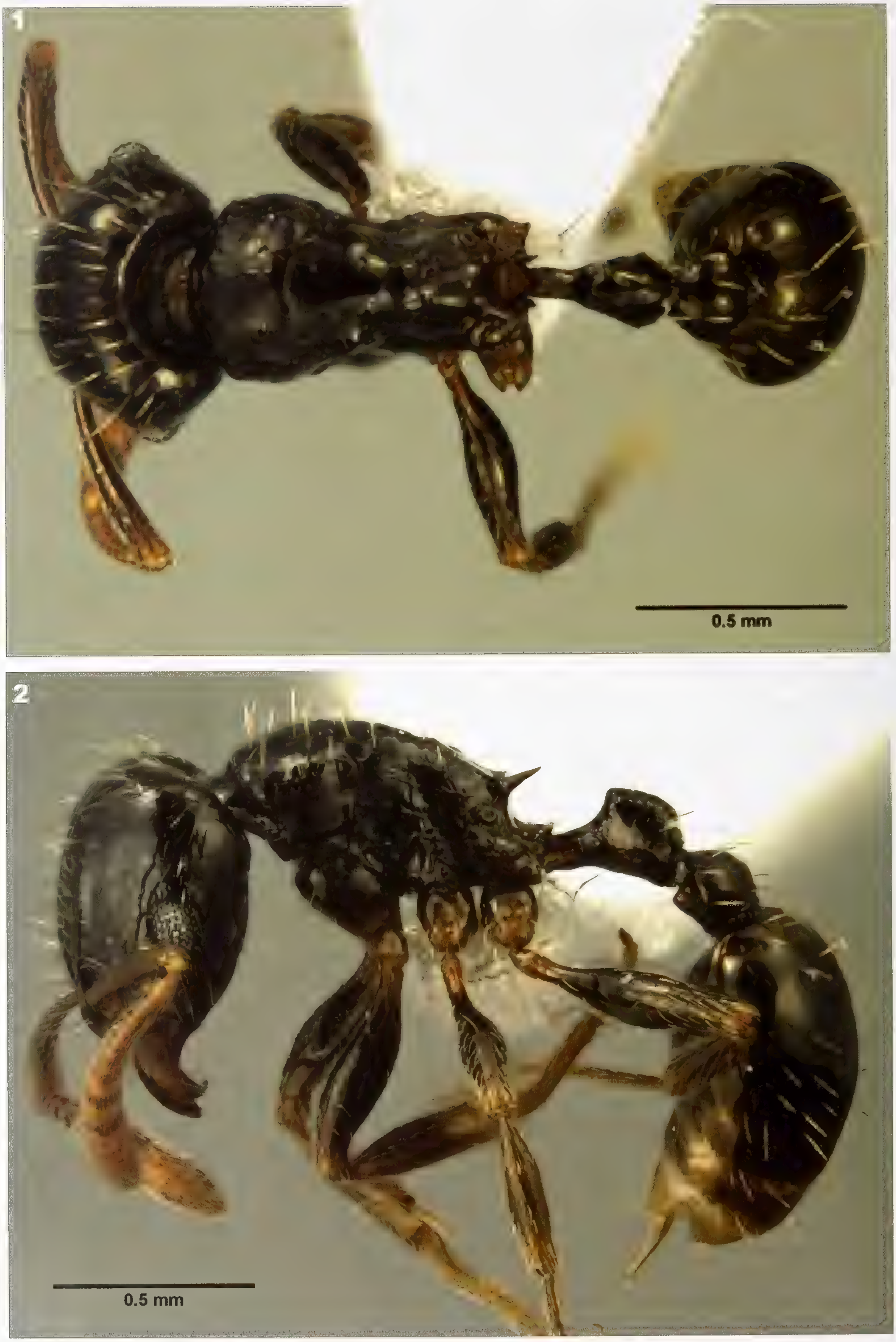

Figs 1–2. *Tetramorium boehmei* sp. n., holotype worker, CASENT0217238. 1 dorsum of body; 2 body in profile.

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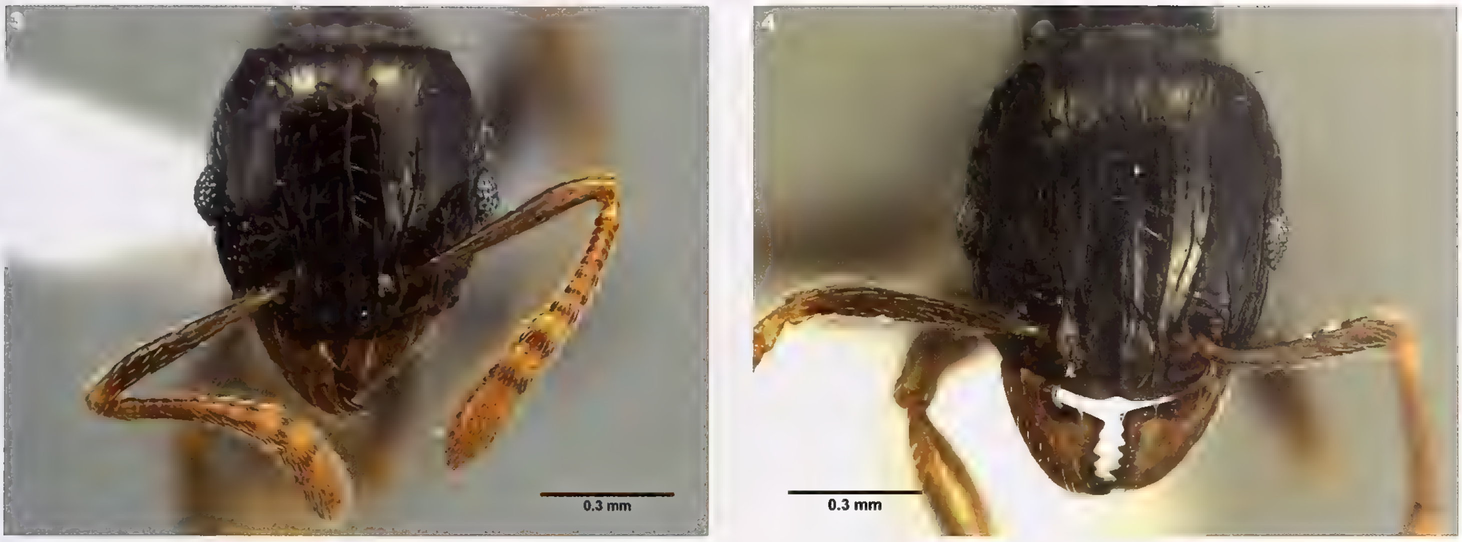

Figs 3–4. *Tetramorium boehmei* sp. n.. 3 holotype worker, CASENT0217238, full-face view of head; 4 paratype worker, CASENT0217239, full-face view of head.

lose, without cross-meshes; occipital rugoreticulum never developed

10. all dorsal body surfaces with numerous standing hairs
11. dorsal surfaces of hind tibiae generally with decumbent to appressed pubescence only, in two species suberect
12. sting appendage triangular, dentiform or pennant-shaped

Prior to this study, the *T. camerunense* species group contained 12 species that were subdivided into two species complexes based on differences in sculpturation (Bolton 1980). The *T. lucayanum* complex, containing four species, can be characterized by the presence of sculptured mandibles, petiole and postpetiole. One or both of the waist segments are generally strongly sculptured. The other and larger complex, the *T. camerunense* complex with eight species, possesses typically unsculptured waist segments and mandibles.

Tetramorium boehmei Hita Garcia & Fischer sp. n.

(Figs 1–6)

Holotype worker, KENYA, Western Province, Kakamega Forest, Colobus, 00° 21' 16" N, 34° 51' 36" E, 1650 m, primary rain forest, hand collected, VII.2009, leg. G. Fischer (NMK: CASENT0217238). Paratype worker, KENYA, Western Province, Kakamega Forest, Salazar, 00° 19' 36" N, 34° 52' 14.6" E, 1650 m, Kakamega Forest survey 2007, Transect 6, primary forest, Winkler leaf litter extraction, 21.VI.2007, leg. M. Peters (ZFMK: CASENT0217239).

Diagnosis. The highly reduced cephalic and mesosomal sculpturation renders *Tetramorium boehmei* straightforwardly recognizable within the *T. camerunense* species group.

DESCRIPTION

HL 0.700–0.772; HW 0.633–0.711; SL 0.533–0.578; EL 0.122–0.139; PW 0.450–0.489; WL 0.822–0.900; PSL 0.150–0.189; PTL 0.194–0.200; PTH 0.211–0.239; PTW 0.178–0.189; PPL 0.189–0.200; PPH 0.194–0.222; PPW 0.250–0.267; CI 90–92; SI 82–84; OI 19–20; PSLI 21–24; PeNI 39–40; LPeI 84–92; DPeI 91–94; PpNI 55–56; LPpI 90–97; DPpI 132–133; PPI 141 (2 measured).

Head longer than wide (CI 90–92). Anterior clypeal margin with small but distinct median notch. Frontal carinae fine and relatively weak, even weaker behind eye level and significantly not reaching occipital margin. Antennal scrobe very weakly developed, nearly vestigial. Antennal scape of moderate length, not reaching posterior margin of head (SI 82–84). Eyes small to moderate (OI 19–20), with 8 to 9 ommatidia in longest row. Metanotal groove not impressed. Propodeal spines moderately sized (PSLI 21–24), relatively thin, spinose and straight. Propodeal lobes small, elongate-triangular and acute, always shorter than propodeal spines. Petiolar node nodiform, in profile weakly higher than long (LPeI 84–92), in dorsal view slightly longer than wide (DPeI 91–94) and posteriorly wider than anteriorly. Postpetiole rounded, in dorsal view around 1.3 times wider than long (DPpI 132–133), and around 1.4 times wider than petiole (PPI 141); in lateral view weakly higher than long (LPpI 90–97). Sting appendage triangular.

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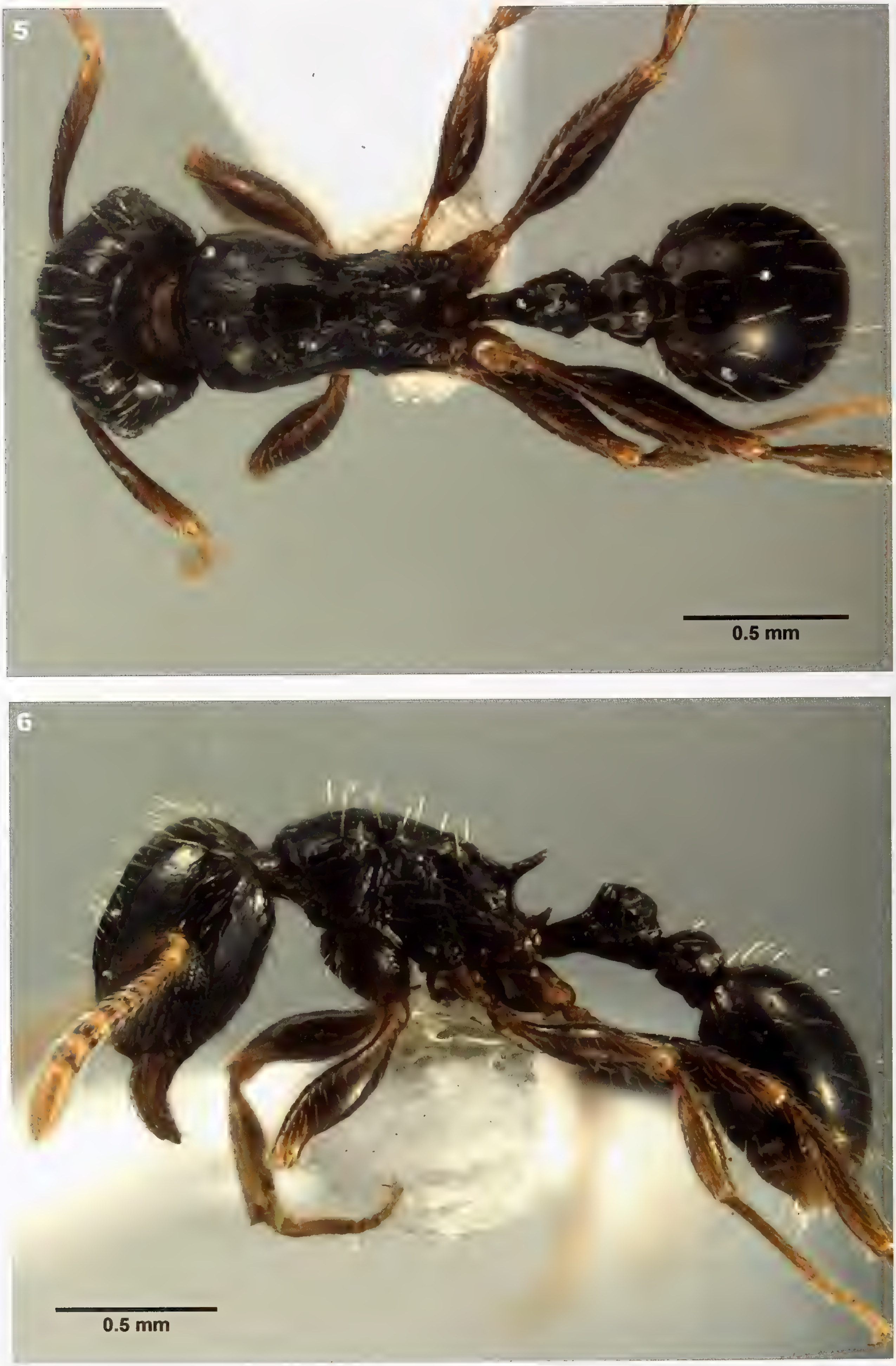

Figs 5–6. *Tetramorium boehmei* sp. n., paratype worker, CASENT0217239. 5 dorsum of body; 6 body in profile.

Mandibles either unsculptured, smooth and shining or finely striate. Clypeus with three longitudinal rugae, median ruga stronger developed than lateral rugae. Cephalic sculpturation greatly reduced, laterally with only weak partial rugulation, mostly smooth and shining; cephalic dorsum with 5–6 very weak and fine, widely spaced longitudinal rugulae between frontal carina, most of them broken along their length and never reaching occipital margin, occipital region unsculptured. Cephalic ground sculpturation absent, generally smooth and shining. Lateral mesosoma anteriorly mostly unsculptured, smooth and shiny, posteriorly with weak irregular rugulation; dorsum of mesosoma unsculptured or with few weak rugulae, or traces of rugulae only, generally smooth and shining. Petiole either completely unsculptured or with traces of sculpture; postpetiole and gaster completely unsculptured, smooth and shiny.

All dorsal surfaces of head, mesosoma, both waist segments and gaster with numerous long, simple, suberect to erect hairs. Fine pubescence on antennal scapes and tibia appressed to subdecumbent.

Head, mesosoma, waist segments, and gaster very dark brown to black, antennae, mandibles, and legs of lighter brownish colour.

Queen and male unknown.

Etymology. The new species is dedicated to Prof. Dr. Wolfgang Böhme from Bonn, Germany, in honour of his nearly four decades of passionate herpetological work at the Zoological Research Museum Koenig in Bonn. Furthermore, with his encouraging, and always interesting, lectures, courses and excursions he had a significant positive influence on the authors leading to their scientific dedication with zoological systematics and the Afrotropical zoogeographical region.

Notes. Generally, it is not recommendable for large and diverse genera as *Tetramorium* to describe single species based only on few specimens outside a comprehensive generic revision. Nevertheless, in the case of *T. boehmei* it seems justified for the following reasons. First, it does fit all group characters and can therefore easily be identified as a *T. camerunense* species group member, either by using the species group key presented above or the one in Bolton (1980). Within the *T. camerunense* species group it obviously belongs to the *T. camerunense* species complex because of the unsculptured petiole and postpetiole. Second, and more importantly, *T. boehmei* shows a remarkable character combination that varies significantly from the other members of the species group, and allows an easy and clear identification. The single best diagnostic character to separate *T. boehmei* from the rest of the group is the almost completely reduced sculpturation on head and mesosoma. This reduction to a few weak rugulae on the cephalic dorsum, and even less sculpturation on the mesosomal dorsum, is unique in the species group. All other species possess a distinctly longitudinally rugose or rugulose head and mesosoma, though variable from species to species, and sometimes irregularly shaped.

It has to be mentioned that the holotype and paratype differ in some aspects that could be considered as sufficient enough to divide them into two different species. First, the mandibular sculpturation is completely smooth and shiny in the holotype while it is longitudinally striate in the paratype. This character is usually species-specific and could be considered as a good diagnostic tool to divide them. Second, the paratype is larger and possesses more sculpture on head and mesosoma than the holotype which appears generally much more smooth and shining. Furthermore, the clypeal notch is distinct in both species but stronger developed in the paratype. However, at present, the observed variation is considered as intraspecific variation until more material becomes available. Apart from the noted differences there is a striking morphological similarity between both specimens and also the morphometric measurements of both are very close. Concluding, based on the analysis of two specimens, it would be premature to describe them as different species.

Currently, the new species seems to be endemic to the Kakamega Forest in Western Kenya where it was sampled in primary forest sites. Considering the high sampling effort to assess the ant fauna of the Kakamega Forest (Hita Garcia et al. 2009), and the only two available specimens of *T. boehmei*, it seems to be a rather rare species. In addition, only little information is available on its biology. One specimen was found in a Winkler leaf litter extraction sample and one was hand collected from the ground. Considering this, the new species could be regarded as a rare terrestrial species, living either in the ground or the leaf litter. Though, it might also be possible that *T. boehmei* lives in the lower vegetation or the canopy, and the two specimens were only accidentally collected by the mentioned methods (the canopy ant fauna was considerably less well sampled by the authors than the ground living ant fauna). At present, taking into account our knowledge of the leaf litter fauna of the Kakamega Forest, we consider the leaf litter hypothesis as more likely. The overall morphological appearance with small to moderate eyes and antennal scapes as well as the strongly reduced body sculpturation are within the genus *Tetramorium* more often found in the leaf litter than in the canopy where species tend to have larger eyes and scapes. However, more specimens from more sampling events are necessary to reveal the preferred stratum of *T. boehmei*. Furthermore, it should be noted that *T. boehmei* was sampled in the two least dis-

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turbed primary forest sites examined in the Kakamega Forest (FHG, unpublished data). This might indicate that the new species prefers undisturbed primary forest and reacts negatively to anthropogenic disturbance like selective logging.

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Homeless mammals from the Ionian and Aegean islands

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Abstract. The paper present information about several mammalian species reported erroneously from the Ionian and Aegean islands and the occurrence of stuffed specimens in museum collections which reveal intriguing stories about their origins, especially about the islands from which they were collected. According to scientific and popular literature, these islands were often not numbered among the original homelands, nor even the territories of the artificial distribution of the species. So it is almost impossible today to understand why and how certain specimens reached these islands, especially in the case of those which were dangerous predators for the livestock, and even humans. This is the case, for example, of the Asia Minor Leopard, *Panthera pardus tulliana* Valenciennes, 1856, which today figures among the collections of the Natural History Museum of the Aegean, in the village of Mytelenii on the island of Samos.

Keywords. museum specimens, Ionian and Aegean islands, continental mammals, Asia Minor leopard.

INTRODUCTION

Scientific travellers and other authors of the past have occasionally reported the diffusion on the Ionian and Aegean islands of several mammalian species today completely unknown among the relative faunal assemblages (Fig. 1). Werner (1928) for example quoted the occurrence of a kind of squirrel on the island of Skyros (Northern Sporades), where he collected a specimen between the villages of Skyros and Linaria which he recognized as *Sciurus lilaeus*. According to Ellerman & Morrison-Scott (1951), this taxon is used to define a Greek subspecies of the red squirrel, *Sciurus vulgaris lilaeus* Miller, 1907, characteristic of the region of Mount Parnassus in continental Greece. Nevertheless, the occurrence of the same species on Skyros was subsequently also recorded by other authors such as Wettstein (1942) or Cheylan (1988) in recent times. On the basis of the authority of Werner, and to an even greater extent that of Wettstein, it is very difficult to refute the truth of these reports, even if red squirrels are today completely unknown on Skyros and the other islands of the Aegean and Ionian basin. Perhaps with the exception of Euboea, the natural occurrence of these rodents is, even on the rest of the Mediterranean insular environments, practically unknown. Their presence on some of these islands, such as Veli Brijuni (Croatia) (Scotti 1980), is essentially regarded as a consequence of recent human intervention (Masseti 2005). Representatives of the genus *Sciurus* Linnaeus, 1758, occur also on Lesbos (Ondrias 1966; Hecht-Markou 1994, 1999; Gavish & Gurnell 1999; Thorington & Hoffman 2005) and the Turkish island of Gökçeada (Imbros) (Özkan 1995, 1999; Gavish & Gurnell 1999). These islands are, however, inhabited by another species of the genus, the Persian squirrel, *Sciurus anomalus* Gueldenstaedt, 1785, whose westernmost continental distribution extends to far-eastern Europe and western Anatolia (Gavish & Gurnell 1999). At the same time, however, there is no evidence to exclude the former diffusion of red squirrels on Skyros, where a population could have existed up to the first half of the 20th century, later becoming extinct. Red squirrels could have been imported by man onto the island from the nearby island of Euboea, where their presence was already reported by Lindermayer (1835). In the light of modern ethnozoological enquiry, it would also appear that red squirrels figure among those mammal species which have been the subject of particular human attention for a variety of cultural purposes. In the Levant, for example, people still eat Persian squirrels and live specimens are regularly sold in the markets (Mendelssohn & Yom-Tov 1999).

SPECIES ERRONEOUSLY REPORTED FROM THE IONIAN AND AEGEAN ARCHIPELAGOS

Travellers of the past have often erroneously reported certain mammalian species from the Greek islands. According to Lindermayer (1835), the blind mole *Talpa caeca* Savi, 1822, was dispersed on Euboea. However this 19th century report strikes a false note, since the species

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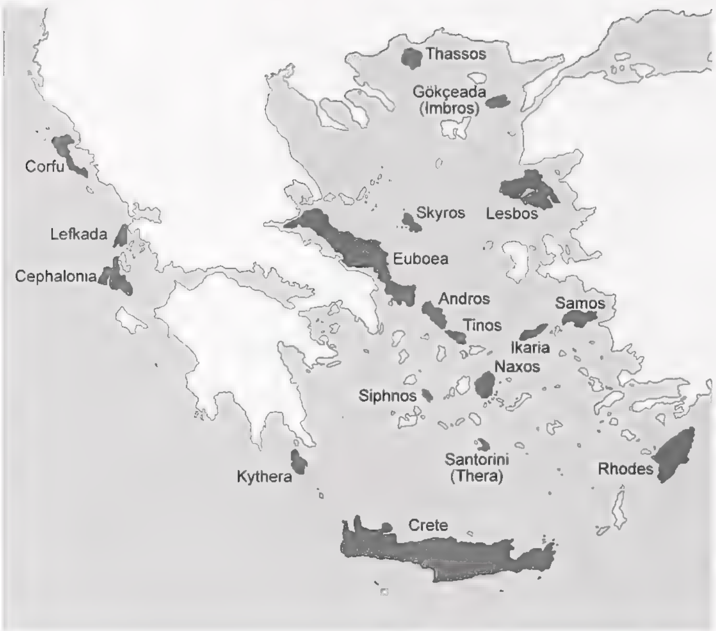

Fig. 1. Map with the locations of the Ionian and Aegean islands mentioned in the text.

is limited in its south-eastern European distributional range to the continental Balkan peninsula. No moles have ever been reported from the eastern Mediterranean islands, with the only exception of the Balkan mole *Talpa stankovici* V. Martino & E. Martino, 1931 on the islands of Corfu (Niethammer 1962, 1990; Kryštufek 1999a) and Cephalonia (Catsadorakis 1985; Giagia-Athanassopoulou 1998; Stamatopoulos, *in verbis*). Wettstein (1942) observed another species, the crested porcupine *Hystrix cristata* Linnaeus, 1758, but mentioned that local people referred to its presence on the Eastern Aegean islands of Ikaria and Lesbos. He (Wettstein 1942) added that this might have been the result of confusion with a hedgehog, the today dispersed Northern white-breasted hedgehog *Erinaceus roumanicus* Barrett-Hamilton, 1900 (Kryštufek et al. 2009). Effectively, the Greek term used to indicate the hedgehog is *skanzohiros*, which means "spiny pig", which is probably the reason of a confusion with the English "porcupine" (and/or the Italian "porcospino" and the French "porc-épic"). Moreover, the common porcupine has never been reported from the Balkan peninsula (Masseti et al. in press), while the Indian crested porcupine, *Hystrix indica* Kerr, 1792 is known from Anatolia with an occurrence further east to the Near East, including Arabia, Kashmir, Nepal and through peninsular India to Sri Lanka (Harrison & Bates 1991). These publications are probably the baseline of several unproven reports. Cheylan (1988) still quoted the occurrence of "*Hystrix cristata*" (sic) on the Eastern Aegean islands of Rhodes, Ikaria and Lesbos. The occurrence of *Microtus subterraneus* (de Sélys-Longchamos, 1836) was reported from Euboea by Cheylan (1988), while Niethammer (1982) and Krystufek (1999b) mentioned it as absent from the entire Mediterranean coast and islands (see also Masseti 2009). A label without specimen, written by Ioannis C. Ondrias himself, in the mammal collection of the University of Patras (coll. no. 3158) reports the occurrence of the common vole *Microtus arvalis* (Pallas, 1779), from the area of Mytilene in south-eastern Lesbos. But, according to Stella Fraguedakis Tsolis (*in litteris* 13th July 2006), this species does not appear to exist or to have ever existed on this island. Furthermore, the specimen to which the label referred has unfortunately been lost. Contrary, the presence of Gunther's vole *M. guentheri* (Danford & Alston, 1880) is known from Lesbos (Stamatopoulos & Ondrias 1995), but according to Kryštufek & & Vohralík (2005) this is the only record from all Mediterranean islands so far.

THE INSULAR EDIBLE DORMICE

Erroneous evaluations, or rather inattentive reading of publications of early authors have supported cultural models which are still difficult to eradicate, e.g. the consideration of the diffusion of several species of glirids in the Greek islands. One example is the erroneously supposed occurrence of the forest dormouse *Dryomys nitedula* (Pallas, 1778). Erhard (1858) reported the occurrence of *Myoxus nitela* Schreber, 1782, a species of glirid, similar in name to the forest dormouse from Andros, Naxos and Siphnos, where it occurred in orchards and orange groves. This report supported the assumption that this rodent occurs on these islands, but in reality the taxonomic classification does not correspond to that of the forest dormouse. According to Ellerman & Morrison-Scott (1951) *Myoxus nitela* is indicated as one of the synonyms of *Eliomys quercinus* (Linnaeus, 1766; garden dormouse), a species currently unknown in the Aegean area and being widespread in the central-western Mediterranean basin. Here it is not found further east than Dalmatia and the north-western Balkan Peninsula. Although according to Kryštufek (1999b), this forest dormouse does not occur on Mediterranean islands, Cheylan (1988) reported it from Euboea. Recently, the presence of the forest dormouse was reported on the island of Andros, which is still an unconfirmed record (Chondropoulos & Fraguedakis-Tsolis, *in verbis*). We have, on the other hand, known for some time of the presence of the edible dormouse on islands such as Crete (Zimmermann 1953; Kahmann 1959; Niethammer & Krapp 1978; Catsadorakis 1994), Euboea (Ondrias 1966), Corfu (Niethammer 1962; Niethammer & Krapp 1978) and Cephalonia (Niethammer & Krapp 1978; Catsadorakis 1985; Giagia-Athanassopoulou 1998). On the latter island, its occurrence has been recently confirmed by H. Pieper (*in litteris*), whereas Dimaki (1999) provided arguments for the existence of the species on Andros. According to H. Alivitzatos & A. Lane (*in verbis*), the edible dormouse is also present on the island of Thassos where they mentioned its occurrence in the surroundings of the village of Panaghia, on 30 August 2000. Wettstein (1942) reports the occurrence of a dormouse, possibly the forest dormouse, from Rhodes, but according to other authors the species is still unknown here (cf. Festa 1914; De Beaux 1929; Zimmermann 1953). A remarkable human impact on the geographical distribution of some dormouse species in the Mediterranean region was observed by Carpaneto & Cristaldi (1994), Colonnelli et al. (2000) and Masseti (2005). The population density can be documented since antiquity through historical and biogeographical analyses, supported by paleontological and archaeozoological data. Furthermore, ethnozoological enquiries document the utilisation of dormice for food or medicine, through traditional captive-breeding techniques, up to very recent historical times.

HOMELESS GREEK ISLAND CARNIVORES IN THE EUROPEAN MUSEUMS

Several European natural history museums conserve material collected on the Greek islands which create problems in the attempt to arrive at their origins. This is the case, in the lynx, *Lynx lynx* (Linnaeus, 1758), collected on the island of Corfu and part of the collection of the Museum Alexander Koenig in Bonn, registered under the collection number ZFMK 93423. The specimen was purchased by Jochen Niethammer during the mammalogical exploration of the island. But the occurrence of the lynx on Corfu was very questionable and immediately resolved by the collector himself. Niethammer reported that he had bought it at the market, where he had been told that it originated from northern Greece, more specifically from Macedonia. In other cases specimens represent species which are in fact completely unknown to the islands which they are reported to originate from. In some cases, species have recently become extinct, like jackals from Corfu represented in the collections of the Museum Koenig (ZFMK 61193, 93420). Dispersed in the Balkan and Anatolian peninsulas, the Golden or Asiatic jackal *Canis aureus* Linnaeus, 1758 has been reported from Corfu (Niethammer 1962; Douma-Petridou 1977; Adamakopoulos et al. 1991; Demeter & Spassov 1993), Cephalonia (Demeter & Spassov 1993), Lefkada (Douma-Petridou 1977; Demeter & Spassov 1993) and Kythera (Jameson 1836, 1937), while other authors mentioned its occurrence on Ikaria (Atanassov 1955) and Skyros (Werner 1928; Wettstein 1942; Atanassov 1955). Ioannidis & Giannatos (1991) surveyed with positive results the island of Samos where jackals exist in the same habitats as in the rest of the southern Balkan Peninsula. Following the account of the expedition to the Greek archipelago published by the botanist Joseph P. de Tournefort (1717), Clarke (1801) observed that "*Samos is infested with wolves*". Anyway, this record should refer to jackals rather than wolves. There is in fact no evidence for the occurrence of the latter canides on the Greek islands of the late Holocene. According to Ioannidis & Giannatos (1991), the jackal no longer exists on Corfu, Kythera, Skyros and Ikaria, where it possibly became extinct in very recent historical times, but jackals vanished from Corfu not before 1991–1992 (Grémillet, *in verbis*). The only Aegean islands where the species still survives are Euboea (Demeter & Spassov 1993) and Samos (Laar & Daan 1967; Douma-Petridou 1977; Adamakopoulos et al. 1991; Ioannidis & Giannatos 1991; Demeter & Spassov 1993; Ioannidis et al. 1996; Dimitropoulos et al. 1998).

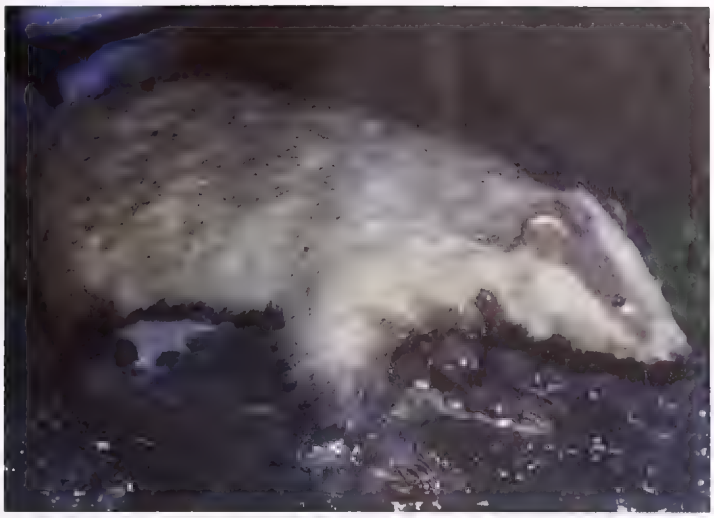

Fig. 2. Stuffed specimen of the badger *Meles meles* collected on the island of Santorini (Thera) in 1859, and part of the collection of the Zoological Museum of the University of Athens (ZMUA 128) (photo Anastasios Legakis; courtesy Zoological Museum of the University of Athens).

Among the collections of the Greek museums, there are several specimens that provoke questions which are still far from having been satisfactorily answered. For example, there is a stuffed badger, *Meles meles* (Linnaeus, 1758) today on display at the Zoological Museum of the University of Athens (ZMUA 128, Fig. 2) and collected on the island of Santorini (Thera) by K. Bassiliou in 1859. This specimen is intriguing because of the old age and it is the only record of the badger from this island. According to Schmalfuss (1991) the species is today unknown from Santorini. If the origin of the ZMUA specimen is correct, the species must have become extinct around the end of the nineteenth century because Douglas (1892) did not mention the badger in his list of the insular mammals. Santorini should therefore be added to the distribution areas of the badger within the Aegean islands. Known in Greek as *asvós*, the badger was recorded from Cephalonia (Catsadorakis 1985), Rhodes (Festa 1914; Tortonese 1973) and Crete (Raulin 1859; Barrett-Hamilton 1899; Bate 1906,

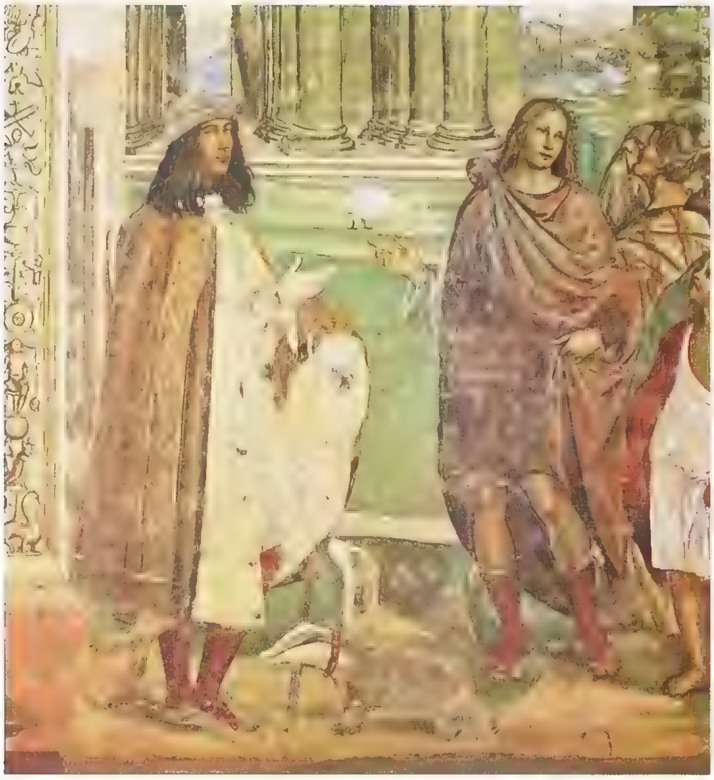

Fig. 3. Detail of the early 16th century wall decoration showing the "Life of St. Benedict" in the Great Cloister of the monastery of Monte Oliveto Maggiore (Siena, Italy) painted by the Italian artist Giovanni Antonio Bazzi.

1913; Miller 1907, 1912; Zimmermann 1953; Ondrias 1965; Ragni et al. 1999) where it is locally indicated by the vernacular term *arkalos*. In the course of the present study, it was possible to confirm its occurrence on the islands of Tinos, where it is locally known as *chakalos* (Gaetlich, pers. com.), Euboea, Crete, Rhodes, and possibly Andros (Gaetlich, pers. com.). There are unconfirmed records of badgers from Siphnos (Erhard 1858; Heldreich 1978; Cheylan 1988), but this does not exclude *a priori* the possibility of a previously more widespread distribution in the Aegean basin, and more specifically on the Cyclades. Moreover, the human practice of the importation of badgers onto the Greek islands is documented since prehistorical times. On Crete the oldest bones of *M. meles* were discovered in the Aceramic Neolithic levels at Knossos, while Ceramic Neolithic and later levels produced numerous remains of the species (Jarman 1996). Other osteological material was found on the site of Aghia Triada, and Kavousi-Vroda and has been respectively referred to the Ancient Minoan period (about 3,000–2,200 B.C.) (Wilkens 1996), and to the Late Minoan III C (Klipper & Snyder 1991; Snyder & Klippel 1996). It is not immediately apparent why human should have wanted to introduce badgers onto the islands, which is suggested because otherwise they would not have been able to pass unobserved on the small boats employed to reach the new territories (Vigne 1988, 1995; Masseti 1995). Since very ancient times, they may have played an important role in human societies, both symbolically and as food. Badgers might also have been utilised for their fur (Masseti 1995). Moreover, in medieval Europe another use of this mustelid has been documented. Wall paintings from the early 16th century (Fig. 3) at the monastery of Monte Oliveto Maggiore (Siena, Italy), painted by the Italian Giovanni Antonio Bazzi, better known as Sodoma, clearly show badgers as pets, very likely representing an authentic status symbol that underscored the affluence and social position of their owner, the painter himself (Carli 1980).

LEOPARDS ON SAMOS – CONCLUDING REMARKS

A stuffed adult leopard (Fig. 4) is on display at the Natural History Museum of the Aegean in Mytelenii, on the Greek island of Samos (Masseti 2000). This specimen previously belonged to the Town Council (Greek: *Nomarkia*) and has been exhibited there for several decades (Ioannidis et al. 1996; Dimitropoulos et al. 1998). On its label it is classified as *kaplani*, with the explanation that this is the Samian terminology indicating a species of panther. However, the word derives from the Turkish term *kaplan*, commonly used in Anatolia to indicate the tiger, and erroneously also the leopard (Danford & Alston 1880). On the basis of available information, it is today not possible to ascertain the age and the origin the specimen. It is said that the leopard was killed on the island between 1870 and 1880, but there is no evidence that this is correct. The title of one of the most famous novels of the contemporary Samian writer Alki Zei, *To kaplani tis vitrinas* (=The *kaplani* of the showcase), better known however as *Wildcat under glass*, was inspired by this leopard. Speaking of her childhood, the author described this *kaplani*, and since she was born in 1936, it can be presumed that the leopard is older. Unfortunately, the Samian specimen is of an unnatural shape because it has been rather inexpertly stuffed, and hardly recalls the form of a living individual. It has a total length of about 235 cm and tail length of 90 cm, apparently proving that this specimen is a large one. But since the skin of felids is extremely elastic, the original dimensions could have been altered during the taxidermic procedure. The coat colour has deteriorated due to bad preservation conditions, and its prolonged display under daylight. The hair of the skin is worn in patches, but it seems that originally the colouration was tawny or buff on the back and paler on the flanks, where it could have merged into the white of the belly. Today, the entire coat is uniform pale, with dark-brown rosettes along the flanks and the back, which are fairly large (about 3–4 cm in diameter), widely spaced and thinly rimmed, with the centres slightly darker than the

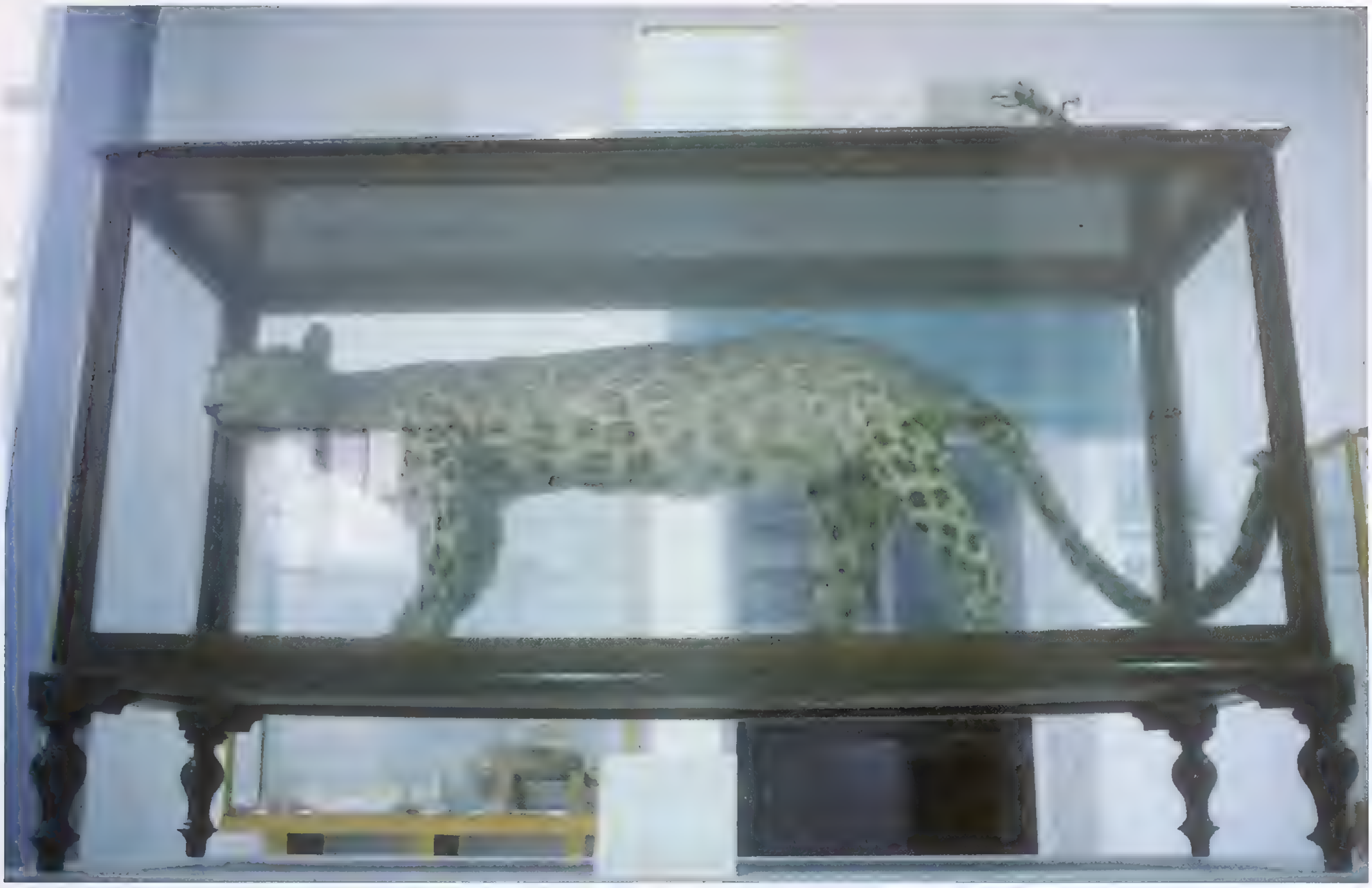

Fig. 4. The stuffed specimen of Asia Minor leopard, *Panthera pardus tulliana* Valenciennes, 1856, shown at the Natural History Museum of the Aegean, Samos (Greece) (photo Marco Masseti; courtesy Natural History Museum of the Aegean, Mytelenii, Samos).

ground tint. The coat is fairly short and full, the hair on the nape is long, and the tail is decidedly bushy. According to the colouration and coat pattern, this specimen could belong to the Anatolian leopard *Panthera pardus tulliana*, as mentioned by Valenciennes (1856), Pocock (1930) and Leyhausen (1991), and clearly distinct from other Near Eastern subspecies (Masseti 2000). It has also been said that the animal arrived at Samos from the opposite coast of Turkey, swimming across the channel separating the island from western Anatolia. In fact there is a deeply-rooted traditional belief on Samos which refer to leopards swimming from Anatolia in various periods. This was reported by Tournefort (1717) who confirmed this legend, observing that: ""*Il y passe quelques tigres qui viennent de terre ferme par le Petit Boghas*". Petit Boghas was the name used at this time to indicate the above mentioned channel. Clarke (1801) followed this observation and mentioned that: "*tigers sometimes arrive from the mainland, after crossing the little Boccaze; thereby confirming all observation made by the author in the former section, with regard to the existence of triggers in Asia Minor*". However, Tournefort (1717) report was probably not based on an own observation, but rather inspired by local people. In any case, since the distance between the island and the mainland is not more than 1.7 km, it cannot be excluded that leopards could have reached the island by swimming, at various times. These felids are good swimmers and could have come e.g. from the Samsundag area (Masseti 2000) which was until the early 1970s the last western Anatolian stronghold of the species (Kumerloeve 1971; Avci 1978; Ulrich & Riffel 1993; Masseti 2000).

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Instructions to authors

Scope

The **Bonn zoological Bulletin** (BzB), formerly "Bonner zoologische Beiträge", is an international, peer-reviewed, open access journal publishing original research articles, reviews, and scientific notes dealing with organismal zoology. Focus of the BzB are (1) taxonomy, (2) systematics and evolution, and (3) biodiversity and biogeography, all with respect to terrestrial animals. Terrestrial animals as understood here include those inhabiting fresh or brackish waters. Contributions from related fields like ecology, morphology, anatomy, physiology or behaviour are welcome when of clear relevance to the focus topics.

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Research articles: Manuscript preparation and submission

Manuscripts should be written in English. For serving readers from the organism's country of origin, bilingual abstracts are welcome. If you plan to submit a manuscript of more than 50 manuscript pages, please contact the editor-in-chief in advance. Please submit your manuscript as electronic file (see paragraph on electronic submission below). Manuscripts should strictly follow the instructions specified below. Manuscripts not compatible with these guidelines will not be taken into consideration.

Format Typing should be double-spaced in 12 pt throughout the text, including tables, figure legends, and reference list. Pages and lines should be numbered consecutively. Short subheadings may structure the text into sections. Do not number headings or subheadings.

Structure Research articles should be organized as follows: Title, Author(s), Address(es) including email address and telephone, Abstract, Key words, Running Title, Introduction, Material and Methods, Results, Discussion (or combined Results and Discussion), Conclusions (optional), Acknowledgements, References, Tables, Figure Captions, Figures (separately numbered and identified), Appendices (if necessary). Footnotes should not be used except in Tables.

Title The title should be brief (30 words limit, ideally shorter) and indicate clearly the field of study and group of animals investigated. The systematic position of taxa listed in the title must be indicated (e.g. "Squamata: Colubridae"). A Running Title (maximum 45 characters inclusive of spaces) should describe the paper's core topic.

Abstract Each manuscript should contain a concise abstract as single paragraph (max. 200 words) summarizing the significant findings, followed by not more than six key words.

References In the text, cited sources should be referred to as follows: Ax (2001), Kim & Lumaret (1989), Holm et al. (1997) – for three or more authors, or, if cited consecutively: (Ax 2001, 2002; Holm et al. 1997; Kim & Lumaret 1989) – please follow exactly the use of commas and semicolons. Do not use commas between author and year (only exception: taxonomic names, in which a comma is placed between author and year).

The list of references should be arranged alphabetically according to the surname of the first author; all authors should be included. Citations of two or more authors should be arranged alphabetically according to the first- and then the following author's surname. When more than one reference is given for a single author or the same combination of authors, these should be arranged chronologically. If citing more than one reference by the same author(s) published in the same year, use a, b, etc. after the year in both, text and reference list (e.g. 2006a, b). The names of journals in the References should be given in full. References "in press" shall only be cited when they have been accepted for publication. Examples of reference style are:

Kottelat M, Whitten T, Kartikasari SN, Wirjoatmodjo S (1993) Freshwater fishes of Western Indonesia and Sulawesi. Periplus Editions, Hong Kong

Mayr E (2000) The biological species concept. Pp. 17–29 in: Wheeler QD & Meier R (eds.) Species Concepts and Phylogenetic Theory – A Debate. Columbia University Press, New York

Parenti RP (2008) A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Beloniformes, Adrianichthyidae). Zoological Journal of the Linnean Society 154: 494–610

Sullivan J (1994) *Bufo boreas*. In: Fire Effects Information System (U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory). Online at http://www.fs.fed.us/database/feis/animals/amphibian/bubo/all.html last accessed on December 28, 2009

Sztencel-Jablonka A, Jones G, Bogdanowicz W (2009) Skull morphology of two cryptic bat species: *Pipistrellus pipistrellus* and *P. pygmaeus* – a 3D geometric morphometrics approach with landmark reconstruction. Acta Chiropterologica 11: 113–126

Authors are kindly requested to make sure that sources listed in the References match those cited in the text. Names of persons who provided unpublished information should be cited by including the initial(s) and city as follows: "(JG Frommen, Bonn, pers. comm. 2009)".

Tables and Figures Tables and Figures should not duplicate information provided in the text. Tables should be numbered consecutively in Arabian numbers in order of their mention in the text (Table 1, Tables 1–3; do not abbreviate "Table(s)"). A brief self-explanatory title should be typed directly above each table, not on a separate page. Do not insert frames, vertical rules, dotted lines or footnotes. Figures (maps, graphs, charts, drawings, photographs etc.) must be numbered consecutively using Arabian numbers in order of their mention in the text (abbreviate "Fig. 1", "Figs 1–3" etc. in the text, but use the full term "Figure(s)" in the captions. If referring to illustrations in cited sources, use "fig. / figs". Grouped figures should be lettered with a lower case block letter in the lower left corner. Scale should be indicated on figures by a scale bar. A fully descriptive caption of each figure should contain all relevant information; captions are to be typed together on a separate page. Colour figures will be published free of charge if contributing significantly to quality and / or readability of the manuscript. The decision to print in colour or black and white any figure submitted in colour will generally be based on the referee's and handling editor's recommendations, but remains with the editor-in-chief and publisher. If appropriate, authors may be asked to group single colour figures into plates. For review, tables and figures should be enclosed to text (preferable one electronic file per manuscript), but may alternatively also be submitted as separate files (jpg, pdf, tiff). At this stage, illustrations of low resolution allowing the referees to follow the contents are sufficient; high-resolution files (jpg, pdf, tiff of photographs, maps etc. at ≥ 300 dpi; line artwork etc. at 600 dpi or in eps format) will be requested after acceptance. Unless otherwise agreed with the editor, single electronic submissions should not exceed 6 MB file size.

Appendix Appendices should be numbered consecutively in Roman numbers, in order of their mention in the text (Appendix I, Appendices I–VI).

Abbreviations Except of very common abbreviations such as mm, kg etc.; all abbreviations should be explained in the Methods section or figure legend if appropriate. Hyphenation or upper case letters for entire words are not permitted. All measurements must be metric units and given to the same decimal, i.e., 5.3–6.0 mm (not: 5.3–6 mm).

Taxonomy Names of animals and the description of new genera or species must follow the current version of the International Code of Zoological Nomenclature (ICZN, available at http://www.iczn.org/iczn/index.jsp). Type specimens should be deposited in recognised institutions; deposition at ZFMK is highly appreciated. Italics are required for species names which are written in full the first time they appear in the text, e.g. *Carassius auratus* (Linnaeus, 1758), but abbreviated at subsequent mention, e.g. *C. auratus*. List names in synonymies as follows: *Attelabus asparagi* Scopoli, 1763 (Scopoli 1763: 36, fig. 113.), and list the source under References. Dichotomous keys are desirable in taxonomic papers.

Statistics Statistics presented should include the name of the test, number of observations or degree of freedom, and probability level ($P > 0.05$, $P < 0.05$, $P > 0.001$, $P < 0.001$). Values of test statistics are not required.

Scientific Notes

Notes should comply with the instructions given above, but have to be (1) confined to a single point or issue of progress, (2) must be short (typically no more than 3 printed pages including illustrations and references), and (3) do not include headings or subheadings. A brief abstract of no more than three lines is required.

Review papers

Reviews should be concise, critical and creative, seeking to summarize the state-of-the-art of complex topics, and stimulate debates and new research initiatives. Review papers should comply with the instructions for preparation of Research articles, with the exception that the main body of text may be structured as appropriate.

Electronic submission

Manuscripts should be submitted as text files (*.doc or *.rtf; *.pdf is welcome for the review process, but for production *.doc or *.rtf will be required) via e-mail (bzb.zfmk@uni-bonn.de) to the editor-in-chief. Alternatively, send a CD. If neither is possible for any reason, please contact the editor-in-chief. The file name must start with the submitting author's last name.

Review process

Each manuscript will be peer-reviewed, generally by two or more referees. Manuscripts should be submitted to the editor-in-chief, and will be handled by the editor dealing with the respective taxon or topic (see list of editors). Authors are encouraged to suggest potential referees for their manuscripts. Final acceptance for publication is in the responsibility of the editor-in-chief. This decision is mainly based on the referees' report and the handling editor's recommendation. Revised manuscripts received more than 6 months after the reviewers' comments had been sent will be treated as new submissions.

Ethical and legal aspects

Authors are obliged to state clearly that they followed the legal regulations and laws for the collection and ethical treatment of animals.

Publication and reprints

Manuscripts will be published online after acceptance as preprint version, which will be replaced by the final pdf after publication of the printed issue of BZB. The corresponding author must clearly state so if preprint online publication is not desired. In that case, only title, authors and the information that this manuscript has been accepted for publication will be made available at that stage. Immediately after publication, the corresponding author will receive an e-mail containing the final pdf. On request (see order form submitted with page proofs), 25 reprints are supplied free of charge. Additional reprints may be purchased on the author's expense.

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Authors preparing manuscripts for BZB should keep in mind the following questions which referees for the journal are asked:

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3. Please grade originality, quality of data, quality of statistical analyses, and quality of interpretation on a scale from 1 = low to 5 = high.
4. Please grade clarity and quality of text, figures and tables from 1 = low to 5 = high.
5. Has the welfare of any experimental animals been adequately taken into account?
6. Does the title aptly and correctly describe the paper?
7. Does the abstract summarize only the significant findings?
8. Is the length of the paper appropriate?
9. Are all (colour) figures and tables necessary and appropriate?

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